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MORPHOLOGY AND ANATOMY OF THE SAURURACEAE. I. FLORAL ANATOMY AND EMBRYOLOGY[1]

M. V. S. RAJU

ABSTRACT

The present paper deals with certain aspects of morphology and anatomy of the Saururaceae. Floral anatomy and embryology suggest a close relationship among the genera. In floral anatomy the genus *Saururus* is the least specialized and *Anemopsis* the most highly specialized. Structure and morphology of inflorescence and also flower suggest the manifestation of certain evolutionary trends, probably guided by reduction, cohesion and adnation. Origin of inferior ovary in the Saururaceae is discussed. Carpels and nature of placentation show certain primitive features. Origin and evolution from apocarpous condition to syncarpous condition of carpels are briefly discussed. Further details will be presented in a separate paper. M. V. S. RAJU, Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

INTRODUCTION

The Saururaceae has been one of the long-neglected angiosperm families in the field of morphology and anatomy. A perusal of the literature shows that earlier investigations have been superficial. In several discussions of comparative morphology and anatomy of the families of the order Piperales and other allied orders, some of the old descriptions of the Saururaceae have been considered. Very often, the family Saururaceae and its composition and affinities have been discussed without much detailed work. In view of this lack of sufficient information, an attempt has been made to investigate in detail some of the salient morphological and anatomical features.

The Saururaceae, according to present knowledge, consists of 6 species—*Saururus cernuus* L., *S. chinensis* (Lour) Baill., *Houttuynia cordata* Thunb., *Anemopsis californica* Hook. & Arn., *Gymnotheca chinensis* Decaisne., and *G. involucrata* P'ei. No material of the last genus was available for this investigation. However, at various stages of description and discussion, previous reports on *Gymnotheca* have been taken into consideration. The present paper deals with floral anatomy and embryology and other related features of the Saururaceae.

Members of the family Saururaceae are perennial aromatic herbs inhabiting moist places. The spirally arranged simple leaves are stipulate (Figs. 1, 5, 8). In *Houttuynia* the stipules are prominent, often enclosing a part of the internode

[1] An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as part of a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

above the node (Fig. 8). In the other genera, they are not prominently visible but are adnate to the petiole and form a sheath around the node as in monocots. The leaves of *Saururus, Gymnotheca* and *Houttuynia* are auriculate to lanceolate and palmately net-veined. In the case of *Anemopsis,* leaves are elliptic-oblong with a conspicuous mid-vein.

Inflorescence

The inflorescence of the Saururaceae is either a terminal spike or a raceme (Figs. 1, 5, 8). In *Saururus* the naked bracteate flowers are often arranged in pairs, a feature which distorts their spiral arrangement. The flowers are adnate to the subtending bract in earlier stages of growth. The flowers of *S. chinensis* are much more sparsely arranged than those of *S. cernuus,* but in most other respects, the inflorescences of the two species are similar (Figs. 12, 13).

The inflorescence of *Houttuynia cordata* has been described in detail by Nozeran (1955). It is a spike with 4 conspicuous bracts at the base (some flowers, however, have small pedicels). Bracts higher up are much reduced to either scales or simple enations. The flowers show various degree of adnation of their pedicels with the bracts. However, in most cases this adnation is not superficially recognizable (Figs. 9, 15). In this species, Nozeran (1955) has reported a progressive transformation of complete flowers into staminate and pistillate ones within the same spike. Similar transformation has been observed by the present author.

Structures of both flower and inflorescence of *Anemopsis* have been described by Quibell (1941). The inflorescence is a highly condensed spike and is subtended by 6–8 petaloid bracts. The young inflorescence axis in early stages resembles a flower covered by bracts. The inflorescence axis is mainly made up of "sunken" pistils (Fig. 16). The bracts, which vary in number, are foliaceous and gradually decrease in size from base upwards (Fig. 5). Except for the lowermost bracts, the rest are adnate to naked flowers.

The inflorescence of *Gymnotheca chinensis* is also a spike, if one follows the terminology of Nozeran (1955). The bracts are not so conspicuous as those of *H. cordata* and *A. californica.* However, the gradual reduction in size of bracts from base upward is similar to the situation in *H. cordata.*

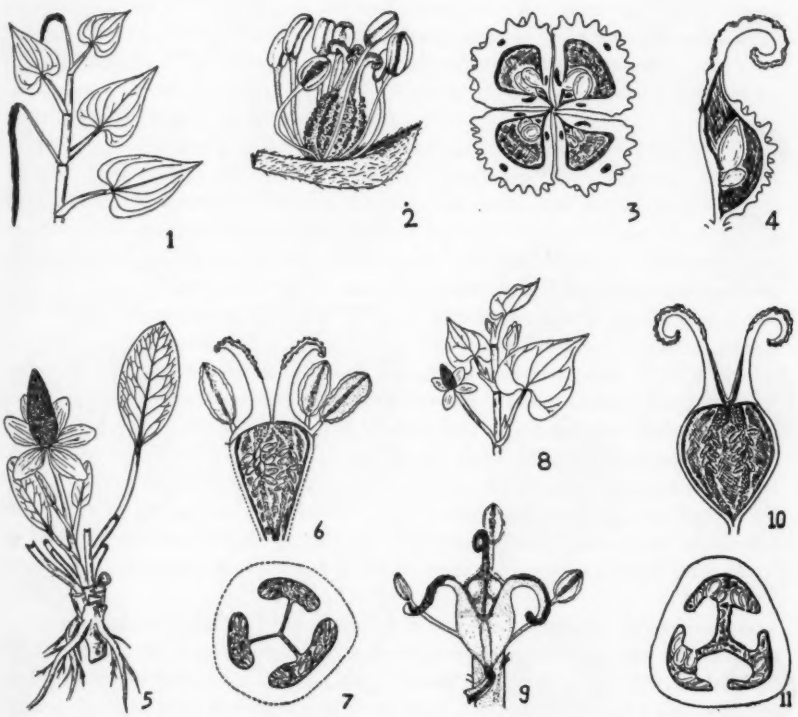
Flower

Flowers of *Saururus,* particularly *S. cernuus* show considerable variation in structure and number. An average flower of *S. cernuus* is pedicellate with 4 simple pistils and 6 stamens. Other combinations like 4–5, 4–7, 4–8, 5–7, 5–8, 3–4, and 3–6 have been observed. Serial sections of flowers of *S. cernuus* show the spiral arrangements of carpels and stamens. Carpels are very closely approximated to one another giving an impression of syncarpy. The stamens are hypogynous and are opposite the carpels (Fig. 2). Pistils show extensive stigmatic crests on adaxial sides of styles (Figs. 2, 4). The stamens are much longer than the styles. In *S. chinensis* flowers show the same variation as *S. cernuus,* but the pistils have shorter styles. Stamens in *S. chinensis* are perigynous and do not exceed the pistils in height.

In *Houttuynia cordata,* the flowers are naked and have small pedicels. These

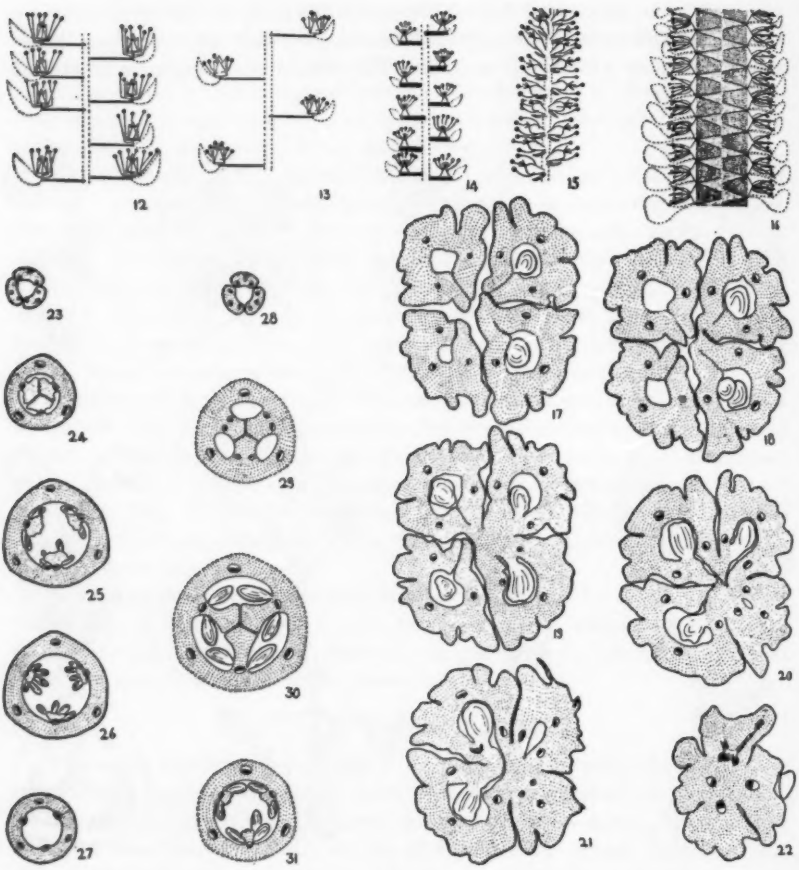
pedicels toward the inflorescence apex are further shortened or the flowers are sessile. The compound pistil is made up of three carpels, and the styles are free with wide stigmatic crests on their adaxial sides (Figs. 9, 10). In the arrangement of flowers, *Gymnotheca* resembles *Houttuynia*. According to the diagram of Decaisne (1845), the flower of *Gymnotheca chinensis* has a 4-partite pistil and 6 epigynous stamens (Fig. 14).

The inflorescence of *Anemopsis californica* has pistils buried in the "inflorescence axis". In these naked flowers, the compound pistil is made up of usually 3 carpels with free styles. The epigynous stamens are usually six in number. However, this number is subject to variation. The petaloid bract appears to be situated



Text Fig. 1. Figs. 1–4. *Saururus cernuus*. Fig. 1. A portion of branch showing the spiral arrangement of leaves and terminal inflorescences. Fig. 2. A flower with bract, stamens and pistils (note the warty structures on ovary). Fig. 3. Sectional view of pistil to show the position of ovules and vascular traces. Fig 4. Longisection of a carpel. Figs. 5–7. *Anemopsis californica*. Fig. 5. A small plant with roots, rhizome, rosette of leaves and an inflorescence. Fig. 6. Longisection of ovary showing placentation, flared margins of stigmatic crest and epigynous stamens. Fig. 7 Transection of same showing parietal placentation and incomplete septa. Figs. 8-11. *Houttuynia cordata*. Fig. 8. A portion of branch with leaves, stipules and inflorescence. Fig 9. A flower with a compound pistil and epicarpellary stamens. Short pedicel of flower is adnate to scale-like bract. Fig. 10. Longisection of pistil showing placentation and stigmatic crest. Fig. 11. Transection of ovary showing parietal placentation.

at the neck of the compound pistil. Developmentally it is adnate to the pistil along its length (Fig. 49). It is also interesting to note that in certain inflorescences bracts show a gradual change from base upwards from a petaloid bract to a petaloid stamen. This also followed by a highly reticulate venation pattern in the lowest bract to a highly reduced "dichotomous pattern" in bracts at the tip of inflorescence.



Text Fig. 2. Figs. 12–16. Diagrammatic sketches of portions of inflorescences of *Saururus cernuus, S. chinensis, Gymnotheca involucrata, Houttuynia cordata,* and *Anemopsis californica* respectively. Figs. 17–22. *Saururus cernuus*—Transverse sections of flower (stamens not included) at different levels to show spiral arrangement of carpels and also placentation, × 80. Figs. 23–27. *Houttuynia cordata*—Transection of compound pistil at different levels (diagrammatic). Figs 28–31. *Anemopsis californica*—Transection of flower (stamens not included) at different levels (diagrammatic).

Anatomy of the Flower

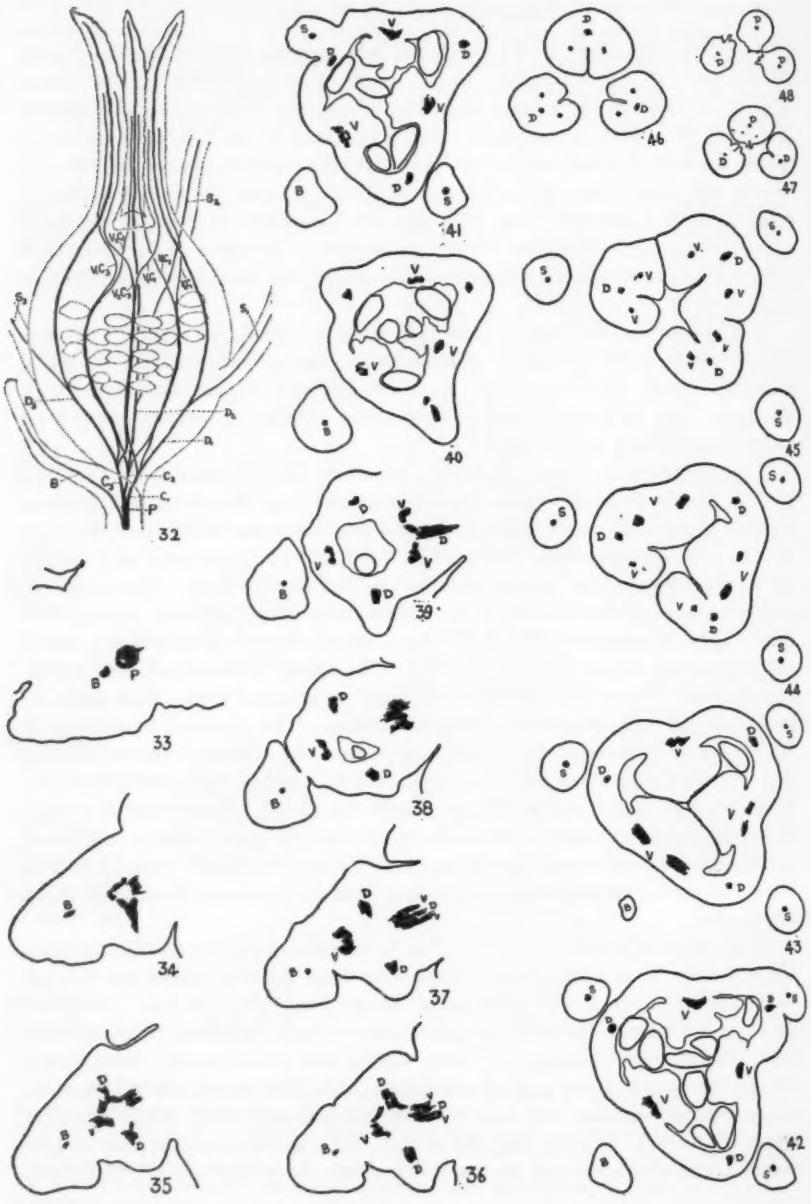
Saururus.—Anatomy of the flower has been recently described for S. *cernuus* by Murthy (1959). Carpellary traces* in the flower originate spirally. Serial sections also indicate the spiral arrangement of carpels. Although ventral margins of carpels are closely approximated or partially fused at the lowermost regions of 'pistil', the ventral traces remain free throughout their course. In certain cases the ventral and dorsal traces of each carpel merge at the apex and appear as though fused to form a common trace. It is also not uncommon to find ventral traces ending near the base of styles. Ventral traces give off branches to the two ovules present in each carpel; placentation in the carpel has been here interpreted as laminar (Figs. 3, 4, 17–22).

The anatomy of the flower of *Saururus chinensis* is similar to that of S. *cernuus* with, however, a few deviations. Stamen traces arise as branches from the dorsal traces of carpels. The ventral trace invariably merges in the stigmatic region with the dorsal trace to form a thick common trace. Unlike S. *cernuus*, there is no conspicuous style in S. *chinensis*.

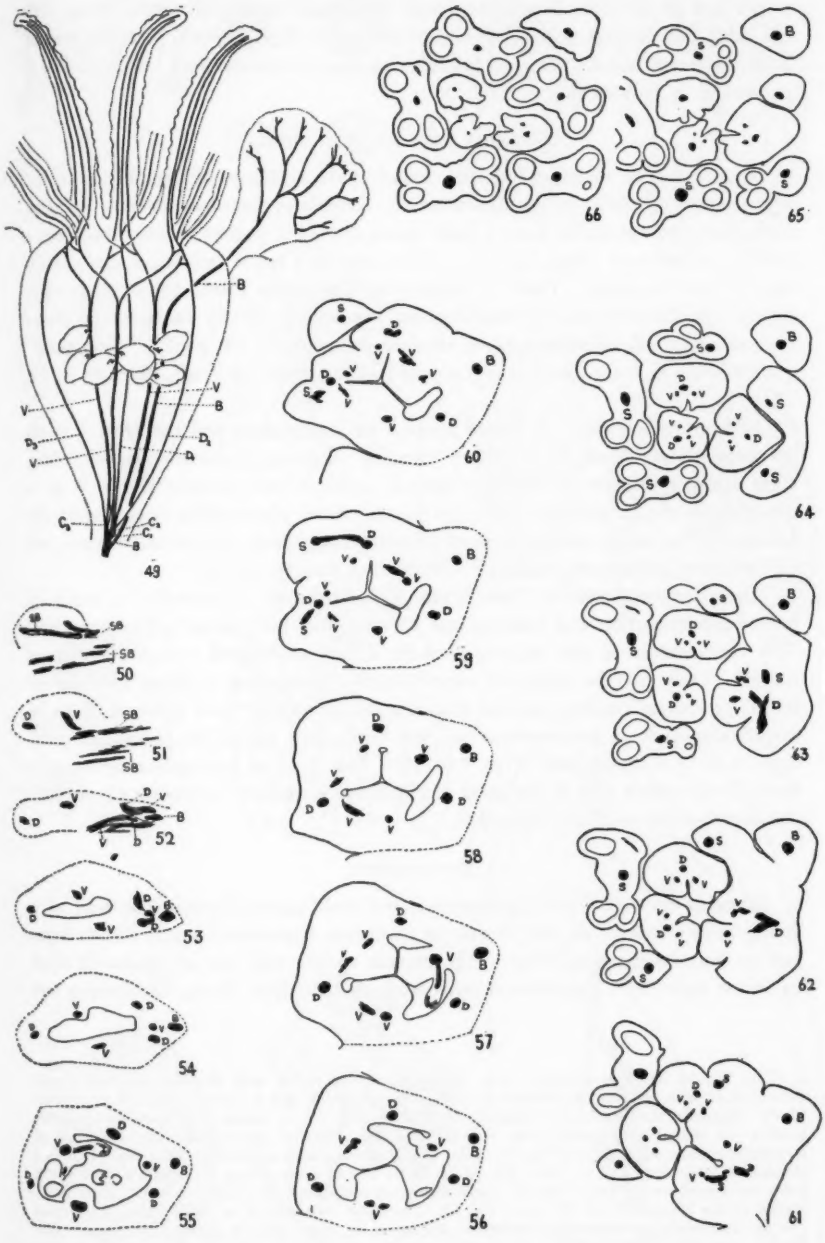
Houttuynia.—The naked flowers are trimerous and bracteate (Fig. 9). The vascular bundle from the inflorescence axis extends into the cortex and becomes the trace for the flower. It branches to form two traces, one leading into the bract and the other into the flower proper (Figs. 32, 33). The bract trace may or may not ramify depending on whether the bract is "leaf-like" or scaly. The remaining trace branches at different levels to form three independent carpellary traces which show a spiral arrangement (Fig. 32). Each carpellary trace gives rise to a dorsal and two ventral traces (Figs. 32, 34–39). The ventral traces of adjacent carpels fuse together to form "compound ventral trace" or placental trace. Each placental trace gives off branches which supply the ovules. The placental trace when it reaches the style bases separates and extends into the respective styles. Ventral traces together with the dorsal trace go into the style and all three remain separate. No instance of their fusion at the tip of style was found. Placentation is parietal and ovules are present only in placental region where the ventral traces have fused to form the placental trace. Stamen traces are formed much later than the ventral traces and arise about the middle of the pistil from the carpellary dorsal trace (Figs. 32, 40–48).

Anemopsis.—Quibell (1941) has given in sufficient detail the vascular anatomy of the flower. As in other genera, a single trace from the inflorescence axis diverges and branches to form a bract trace and a "flower trace" (Figs. 49-52). Although the bract is adnate to the pistil, the bract-trace is free throughout (Figs. 49–66). Each "flower trace" branches to form ventral and dorsal traces. Each carpel receives two ventral traces and a dorsal trace. As in *Houttuynia*, ventral traces of adjacent carpels immediately fuse to form the placental trace whose branches supply the ovules. At about the base of style, the placental traces separate to give ventral traces which pass into the respective styles. Each ventral trace, on its way

* For the sake of convenience the term 'trace' has been used in describing the vasculature of different organs of flowers.



Text Fig. 3. *Houttuynia cordata*. Fig. 32. Diagrammatic sketch of a flower showing vascular traces. Figs. 33–48. Transections of flower at different levels to show vascular anatomy of the flower (B, bract trace; $C_{1, 2, 3}$, traces of three carpels; D, dorsal trace of carpel; $D_{1, 2, 3}$, dorsal trace or common trace of dorsal trace of carpel and stamen trace; P, pedicel trace; S, stamen; $S_{1, 2, 3}$, stamen traces; $V_1 C_1$, $V_2 C_1$, $V_1 C_2$, $V_2 C_2$, $V_1 C_3$, $V_2 C_3$, ventral traces of respective carpels; V, ventral trace), × 100.



Text Fig. 4. *Anemopsis californica.* Fig. 49. Diagrammatic sketch of a flower to show vascular traces. Figs. 50–66. Transections at different levels of a flower showing vascular traces (B, bract; C_1, 2, 3, carpel traces; D, D_1, D_2, D_3, dorsal traces; SB, axial bundle of inflorescence; S, stamen trace; V, ventral trace), × 100.

to the base of the style, is connected with the dorsal trace. The dorsal trace with the other two ventral traces extend into the style (Figs. 58–66). At the base of style the dorsal bundle gives off branches to one or two stamens. Placentation is parietal as in *Houttuynia.*

Carpels and Placentation

A considerable variation has been found in the structure of carpels and in the organization of pistils in the Saururaceae. Carpels in *Saururus cernuus* are free throughout except at the base, a little above the short pedicel where they show a lateral concrescence (Figs. 17–22). They arise in a spiral fashion, a fact clearly seen in serial sections. There is considerable elongation above the ovule-bearing region. In *Houttuynia, Gymnotheca* and *Anemopsis,* clearly recognizable stylar regions are found. Furthermore, in all these three genera, the pistil is "compound" (in the sense that the ovary is syncarpous and the styles are free) (Figs. 6, 7, 10, 11).

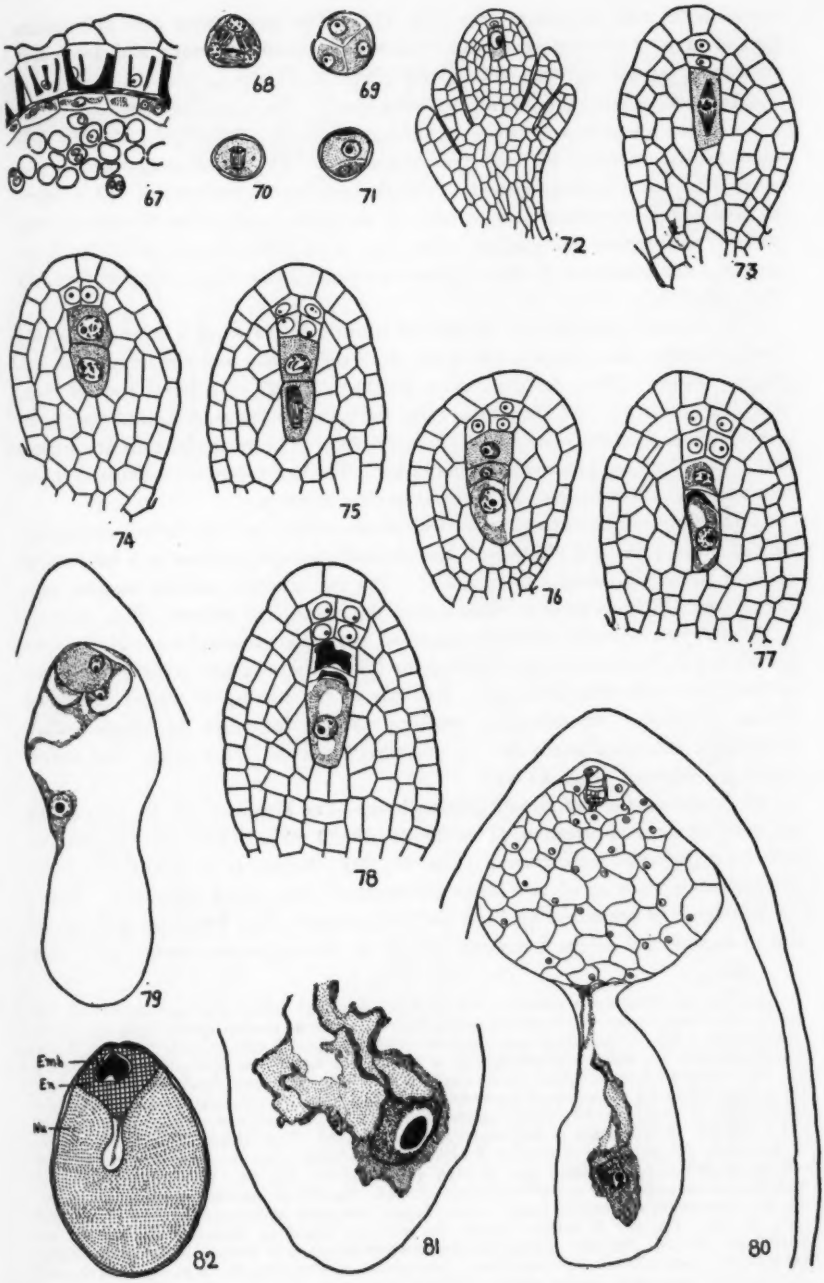
In *Saururus cernuus,* the folded laminae are conspicuous and the ventral traces are present away from the carpellary margins. During organization of the pistil, these laminar margins of adjacent carpels undergo concrescence which is to a considerable extent mistaken for axile placentation; placentation here is actually laminar. The lateral concrescence of adjacent carpels may be attributed to a case of "incipient syncarpous tendency" (Bailey and Swamy, 1951).

The compound pistil of *Houttuynia* and *Anemopsis* is formed as a result of lateral approximation and concrescence of carpellary margins of adjacent carpels. This concrescence is also accompanied by fusion of ventral traces of adjacent carpels. Only in this region of concrescence of carpellary margins and also of lateral or ventral traces is parietal placentation organized. The sterile margins of carpels also undergo concrescence to form septa; as a result the compound pistil appears to be three-loculed (Figs. 23–31). This kind of incomplete septation is found in the upper part of the pistil of *Houttuynia cordata;* it extends almost half the depth of the pistil in *Anemopsis.*

Embryology

Saururus cernuus.—Microsporogenesis and male gametophyte.—The wall of a young anther consists of four layers, an epidermis, hypodermal layer, middle layer and an innermost tapetal layer. The mature anther wall has an epidermis with cutinized outer wall, hypodermal layer with characteristic fibrous thickening and

Text Fig. 5. *Saururus cernuus.* Fig. 67. A portion of anther wall showing epidermis, hypodermal layer with endothecial thickening, crushed middle layer, and a tepetal layer, × 333. Figs. 68–71. Stages in the formation of microspore, × 833. Fig. 72. A young ovule showing megaspore mother cell and primary parietal cell, × 333. Fig. 73. Nucellus showing division of nucleus of megaspore mother cell, × 666. Fig. 74. Same at a later stage with a dyad, × 666. Fig. 75. Shows division of lower dyad cell, × 666. Fig. 76. A linear row of three cells or a "triad", the lowermost being the megaspore, × 666. Fig. 77. Degeneration of middle cell of a linear "triad". Note vacuolation in the lowermost cell, × 666. Fig. 78. The upper two cells of a "triad" have degenerated and the lowermost has become the functional megaspore, × 666. Fig. 79. Mature embryo sac with the egg apparatus and secondary nucleus, × 666. Fig. 80. Longisection of a young seed showing embryo, cellular endosperm and a lower caecum containing a hypertrophied nucleus, × 147. Fig. 81. An enlarged view of a hypertrophied nucleus in a caecum, × 666. Fig. 82. Longisection of seed showing cellular endosperm, embryo and perisperm (Emb, embryo; En, endosperm; Nu, nucellus or perisperm), × 35.


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tapetal layer with binucleate cells (Fig. 67). The sporogenous cells differentiate themselves into microspore mother cells which undergo meiosis and form first microspore tetrads and then microspores (Figs. 68–71).

Megasporogenesis and female gametophyte.—The crassinucellate ovules are orthotropous-bitegmic and borne on laminar placentae (Figs. 3, 4, 19–21). The micropyle is organized by both the integuments. The outer integument is two layered; the inner is three layered. A single hypodermal archesporial cell is differentiated in a young ovular primordium. It undergoes a transverse division to form primary sporogenous and parietal cells (Fig. 72). The primary parietal cell, by anticlinal and transverse divisions, forms a parietal tissue of about 8 superposed cells (Figs. 73–78).

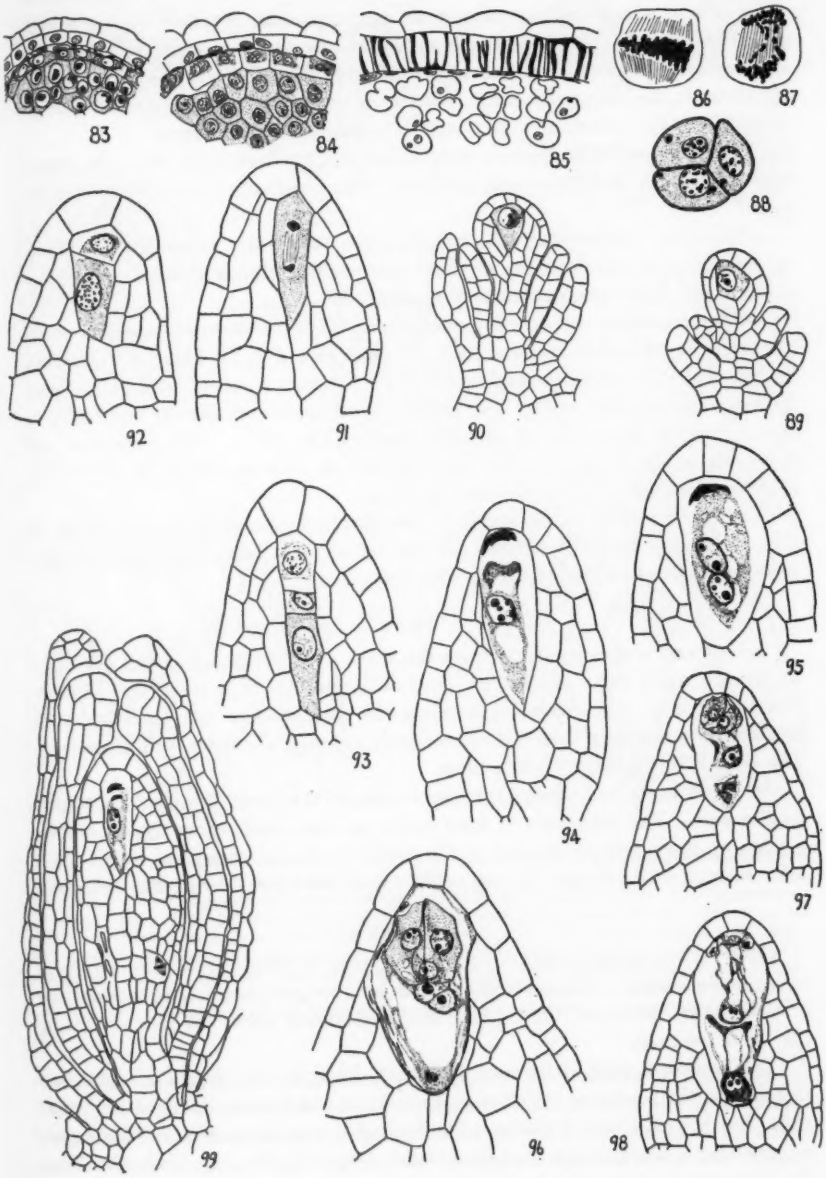
The primary sporogenous cell divides meiotically to form a dyad (Fig. 74). During further development, the lower dyad cell divides and the upper does not (Figs. 75–76). Thus, the dyad gives rise to a "triad" or a linear row of three cells (Figs. 76, 77). Of these three cells, the upper two degenerate and the lowermost develops into the embryo-sac (Figs. 77–79). The antipodal cells are ephemeral and seldom seen in a mature embryo sac. The egg apparatus is situated at the micropylar end and no case of fertilization was observed.

Endosperm.—The endosperm nucleus divides transversely to form a micropylar chamber and a chalazal chamber. The chalazal chamber behaves as a haustorium and the nucleus becomes hypertrophied. The mature seed encloses massive perisperm and a little endosperm surrounding the developing embryo (Figs. 80–82).

Houttuynia cordata.—Microsporogenesis and male gametophyte.—Microsporogenesis and male gametophyte development follow the sequence given for *Saururus cernuus*, but with some differences. Division of the microspore mother cell shows various cytological abnormalities resulting in the formation of sterile pollen. Frequently, micronuclei are seen in microspore tetrads. Very rarely free microspores are observed (Figs. 83–88).

Megasporogenesis and female gametophyte.—The bitegmic orthotropous ovules are borne on parietal placentae (Figs. 25, 26, 89–90, 99). The ovular primordium shows a hypodermal archesporium (Figs. 89, 90). Similar to *S. cernuus*, the outer integument is made up of two layers and inner of three layers (Fig. 99). Again, the micropyle is organized by both the integuments (Fig. 99). An archesporial cell of hypodermal origin functions directly as the megaspore mother cell (Figs.

Text Fig. 6. *Houttuynia cordata.* Fig. 83. A portion of anther showing anther wall and sporogenous tissue; anther wall shows epidermis, hypodermal layer, crushed middle layer and tapetal layer, × 333. Fig. 84. Same at a later stage; note binucleate tapetal cells, × 333. Fig. 85. Mature anther wall showing endothecial thickenings in hypodermal layer; note also microspores, × 333. Fig. 86. Metaphase I in microspore mother cell, × 666. Fig. 87. Same showing anaphase I; note the irregularity in the movement of chromosomes, × 666. Fig. 88. Microspore tetrad with a few micronuclei, × 666. Fig. 89. Ovular primordium with integumental and archesporial initials, × 333. Fig. 90. A later stage of the same, × 333. Fig. 91. First division of archesporial cell, × 666. Fig. 92. A portion of nucellus showing a dyad, × 666. Fig. 93. Same showing the lower cell has divided to form a linear row of three cells, × 666. Fig. 94. Uninucleate embryo sac with degenerated upper dyad cell and megaspore, × 666. Fig. 95. A binucleate embryo sac, × 666. Fig. 96. An embryo sac showing hooked synergids, egg, two polar nucleii and degenerated antipodal cells, × 666. Fig. 97. A mature embryo sac with egg apparatus, secondary nucleus and antipodal cells, × 333. Fig. 98. A stage showing probably zygote; first division of endosperm nucleus has resulted in two cells, the lower one being a haustorium, × 333. Fig. 99. A young ovule showing the developing megaspore, massive nucellus, and two integuments, inner three-layered and outer two-layered, × 133.


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91–98). The megaspore mother cell divides meiotically to give a linear row of three cells of which the lowermost is the megaspore that develops into the embryo sac (Figs. 91–98). Antipodal cells in the mature embryo sac are epheremal but in some cases these cells are seen in mature embryo sacs (Figs. 96–97). The egg apparatus in the micropylar end is made up of an egg cell and two hooked synergid cells (Fig. 96). Here, also, fertilization stages were not observed.

Endosperm.—The endosperm behaves as in *S. cernuus* (Fig. 98). In mature seeds often only endosperm and perisperm were observed. The embryo was not seen.

Anemopsis californica.—Microsporogenesis and male gametophyte.—Microsporogenesis and development of male gametophyte simulate those of *Saururus cernuus* and *Houttuynia cordata* (Figs. 100–105).

Megasporogenesis and female gametophyte.—The orthotropous bitegmic ovules are found on parietal placentae as in *H. cordata* (Figs. 6–7, 30–31). A hypodermal archesporial cell is differentiated and divides to form a parietal cell and primary sporogenous cell (Fig. 106). The primary sporogenous cell divides meiotically to give a row of three cells as in other genera (Fig. 107). The lowermost cell functions as the megaspore and develops into an embryo sac (Figs. 107–110). Stages in fertilization have not been observed.

Endosperm.—The earlier stages of endosperm development are like those of *Houttuynia* and *Saururus cernuus*. In the mature seed, massive perisperm, degenerated embryo and endosperm were observed.

Fruit

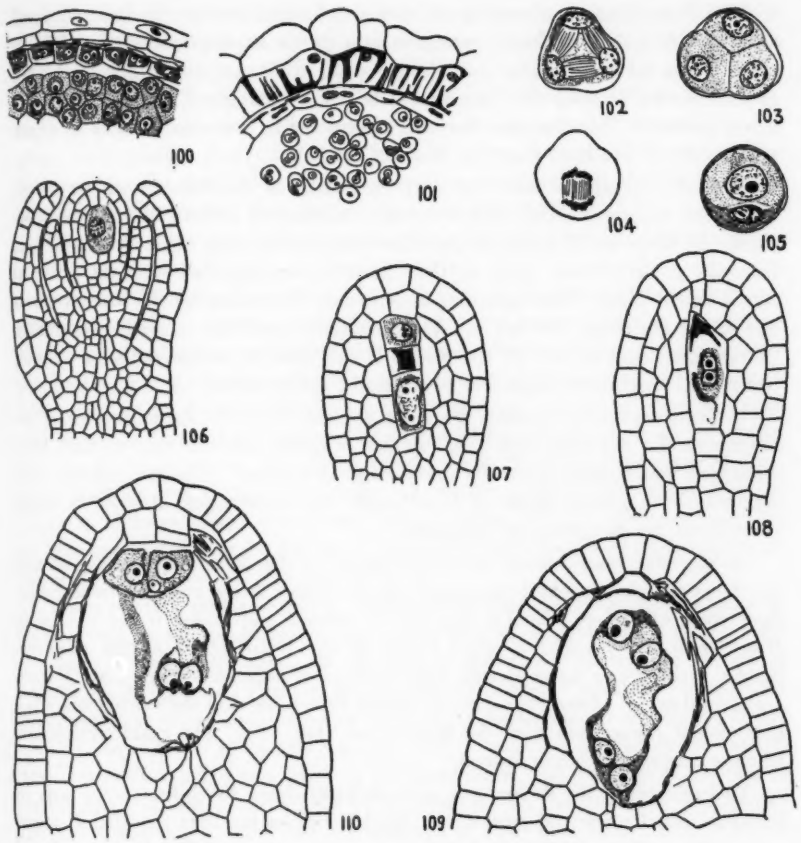
In *Saururus* simple pistils organize the fruit. The pericarp becomes dry-fleshy enclosing a single seed. No case of fruit dehiscence has been observed. Furthermore, there is no stony endocarp developed in the pericarp. On the other hand, seed coat becomes very hard and often closely abutting the inner wall of pericarp. The fruit is here interpreted as a berry.

In *Houttaynia* and *Anemopsis* the fruits are dehiscent capsules with many smaller seeds. The dehiscence of fruit occurs at the apical region by the disintegration of fused ventral margins in the middle region of three free styles. In a dehisced fruit a circular port is seen at the top of the ovary leaving the styles free.

Discussion

Observations on inflorescence of the six species of Saururaceae show an interesting evolutionary trend, probably guided by two processes: 1. reduction, and 2. cohesion and adnation. Of the four genera, *Saururus* shows the least change by the above processes.

The "common stalk" of flower and bract shows various degree of reduction. In *Saururus* the "common stalk" is much elongated and shows stages of its reduction. Further reduction of the same has resulted in a condition seen in *Houttuynia* in possessing a recognizable "common stalk" (Figs. 12, 13, 15). *Anemopsis,* on the other hand, shows the final culmination where the pistils appear embedded in the "inflorescence axis" and the bract appears to be situated at the top of the ovary (Figs. 16, 49). In all genera this process of reduction is associated with



Text Fig. 7. *Anemopsis californica*. Fig. 100. A portion of anther wall showing epidermis, hypodermal layer, crushed middle and tapetal layers surrounding the sporogenous tissue, × 333. Fig. 101. same at a later stage showing endothecial thickenings in the hypodermis; two-celled microspores are seen, × 333. Figs. 102–105. Stages in the formation of microspores, × 666. Fig. 106. A young ovule showing megaspore mother cell and two integuments; note parietal cells, × 333. Fig. 107. A portion of nucellus showing a linear row of 3 cells of which the lowermost develops into an embryo sac, × 666. Fig 108. Same at a later stage showing a 2-nucleate embryo sac with upper two degenerated cells, × 666. Fig. 109. A portion of nucellus with a 4-nucleate embryo sac, × 666. Fig. 110. Mature embryo sac with egg apparatus, two polars and 3 degenerating antipodals, × 666.

concomitant cohesion and adnation of floral parts. By a process of reduction in the number and cohesion of carpels, the polycarpellate condition seen in *Saururus* has resulted in the three or four carpelled syncarpous condition found in the other genera. This change has been accompanied by the adnation of stamens to carpels and is exhibited by *Houttuynia*, *Gymnotheca* and *Anemopsis*. The genus *Anemopsis* has an inferior ovary, a feature that has resulted by their "sinking into" the inflorescence axis.

The phenomena mentioned above may also be explained in the light of floral anatomy. Although the bract appears to be a simple structure, it is very difficult to see where the bract begins and where it ends. It is morphologically intriguing to consider the trace of the "common stalk" as a "compound" one of bract and flower pedicel. This condition has been interpreted in *Saururus cernuus* as a case of adnation of flower to bract, by Murthy (1959).

Present observations show that only the pedicel of the flower is adnate to the bract; this feature is evidenced by vascular anatomy of *Houttuynia* and *Gymnotheca*. In *Saururus, Houttuynia* and *Gymnotheca*, the bract tends to remain free from the flower proper. But, in the case of *Anemopsis*, however, the bract is adnate to the pistil. This feature is of secondary derivation for the bract trace is completely free from the flower. This secondary condition is, probably, due to "development sinking-in" of the pistil. It can also be interpreted as a case of lateral concrescence of compound pistils in the inflorescence.

In *Saururus cernuus*, stamen traces are formed before the carpellary traces are differentiated. But in S. *chinensis*, vascular anatomy indicates that stamens have originated subsequently from the dorsal carpellary trace. This specialization has proceeded in increasing degree in *Houttuynia, Gymnotheca* and *Anemopsis* where the stamens are perigynous or epigynous.

In *Saururus* ventral traces are as prominent as the dorsal traces; they remain free from one another throughout their course except at the stylar tip where they show signs of fusion. Similar behavior of ventral and dorsal traces is seen in *Houttuynia* and *Anemopsis;* their fusion in the stylar tip is seldom observed. Besides, in these two latter genera, ventral traces of adjacent carpels fuse to form a placental trace. *Anemopsis* shows a unique feature in that the ventral trace has independent connections with the dorsal trace (Fig. 49). The exact significance of these connections is not known.

To begin with, the flower gets a single trace from the inflorescence axis in *Saururus, Houttuynia* and *Anemopsis*. Such a feature has been reported in many angiosperms. Puri (1951) in his review paper suggested that highly reduced flowers received just one trace. Whether this condition is simple by primitiveness or by reduction remains to be critically examined. As far as the present observations go, it seems that traces of different organs have undergone fusion to form a single composite trace.

The Saururaceae show both hypogenous and epigynous conditions. The problem then arises as to how the epigynous condition has been achieved. The problem of origin of the inferior ovary has been highly debated for a long time. Douglas (1944) in her comprehensive review has discussed different views regarding morphology of the inferior ovary. Of the many views postulated, only two have remained prominent; they are appendicular and axial views.

It is beyond doubt that in all genera of Saururaceae except *Saururus cernuus* stamens have fused with the carpels. In *Houttuynia* and S. *chinensis* stamens are situated half way up on the pistil. *Anemopsis* and *Gymnotheca* have their stamens on the ovary just below the styles. These clearly show that concrescence of certain

floral parts (here stamens) with the pistils has given rise to epigyny. This is in support of the views expressed by van Tieghem (see Puri, 1951, 1952; Eames, 1931).

In *Anemopsis*, besides the fusion of stamens with the ovary, there is developmentally a concrescence of pistils resulting in a massive spike. This condition has given an impression that pistils have "sunken". Adnation of the bract, with its free trace, to the pistil is an additional evidence to show that the ovary wall is made up of tissues other than that of the ovary wall itself.

Prior to syncarpy and epigyny, profound morphological and anatomical changes have taken place in flowers of the Saururaceae. These changes have been well preserved in the genus *Saururus*. The carpels with their respective stamens are arranged "spirally". The last-formed carpel does not possess a stamen or stamens. This detail suggests that the flowers of *S. cernuus*, adnate to bracts, are not actually simple; they are, probably, derived from a structure similar to an "inflorescence". Absence of an axial tissue, development of a terminal normal or abortive carpel with or without a stamen or stamens, and close telescoping of simple pistils suggest that the flower is of the "sympodial type". Each flower then represented by a carpel with its own stamen or stamens. A similar analogy can be traced in the flowers of Chloranthaceae (Cardemoy, 1863; Hooker, 1890). However, this idea has been contradicted on the basis of the absence of supernumerary structures in the flowers of Chloranthaceae (Swamy, 1953).

The successive arrangements of simple pistils with their associated stamen or stamens lead to two problems—nature of epigyny or perigyny in a simple pistil and same in compound pistil. In the case of *Saururus chinensis* the stamen or stamens are perigynous. This can be interpreted as a case of adnation. Syncarpous gynoecium also shows perigynous and epigynous conditions. It is difficult to say whether the cohesion of carpels appeared first or adnation of stamens to carpels. Available evidences, however, show in the Saururaceae that adnation of stamens to carpels appeared first as exemplified by *S. chinensis*. So, the flowers of *Hauttuynia* and *Anemopsis* suggest that they are made up of three independent flowers which have undergone phylogenetic fusion. This is also amply evidenced by floral anatomy.

The above interpretations further lead to the problem whether the pistil is appendicular or axial. Vascular anatomy shows that there is nowhere in the ovary a residual trace or an axis around which carpels are arranged. The vascular elements are completely used up by the differentiated carpels. It is on this basis that flowers of Saururaceae have been interpreted as condensed inflorescence of the "sympodial type" simulating to a considerable extent vegetative branches where sympodial growth prevails. Anatomical evidences do not, however, give a correct picture of inferior ovary. Developmental studies are necessary for the interpretation of inferior ovary in some members of Saururaceae.

The trends of specialization postulated by Bailey and Swamy (1951) for the ranalian carpel have recently been useful in interpreting some primitive carpels. Although carpels of *Houttuynia* and *Anemopsis* are quite specialized, the conduplicate nature is still present in their styles which have flared-out stigmatic crests.

Although ontogenetic studies have not been made, available observations indicate that the ovule-bearing capacity of the carpel has brought several modifications in its train. The closure of carpels has occurred in the basal or ovule-bearing part leaving behind an extensive stigmatic crest. The stigmatic crest is supplied by both dorsal and ventral bundles. This feature is seen in *Saururus, Houttuynia* and *Anemopsis*. In some of the carpels, particularly of *S. cernuus*, retraction of ventral traces from stigmatic region toward the ovule-bearing part may be noticed. This retraction leaves a short style between ovary and stigma. In the case of *S. chinensis*, the stigmatic crest is supplied by both ventral and dorsal traces; it is situated just above the ovule-bearing part. This progressive phylogenetic specialization leading to the formation of a style between stigma and ovary is exhibited by the carpels of *Saururus, Houttuynia* and *Anemopsis*.

Superimposed on the evolutionary specialization mentioned above there is concomitant lateral concrescence of carpels resulting in a compound pistil. Furthermore, the "spiral" arrangement of carpels becomes less and less clear. Thus, in the development of pistils, simple or compound, several independent trends of specialization have occurred simultaneously in the Saururaceae.

Placentation in the Saururaceae is of two types, laminar and parietal. Laminar placentation is found in *Saururus* and parietal placentation in *Houttuynia* and *Anemopsis*. Bailey and Swamy (1951) after an extensive survey of carpels in the Ranales have come to the conclusion that carpels with laminar placentation are primitive and show various trends of specialization leading toward other types of placentation. A detailed study of carpels of *Saururus* has shown not only a laminar placentation but also different degrees of incipient syncarpous tendencies. The carpellary margins undergo concrescence or close approximation. This concrescence of carpellary margins does not occur at one level since they are arranged spirally. Axial tissue that is seen at the base of carpels is actually a composite of different carpellary margins. As a consequence, the pistil appears to be compound with more than one locule. In fact, this condition probably led several taxonomists to interpret this placentation as axile (Bailey, 1958; Lawrence, 1951; Benson, 1957).

From this basic laminar placentation, parietal placentation of *Houttuynia* and *Anemopsis* can be derived. The presence of free styles in the pistils of the above two genera shows that lateral concrescence of adjacent carpels has occurred in the ovule-bearing parts of carpels. Closely approximated partitions appear in the locule of the ovary of *Houttuynia* and *Anemopsis*. These partitions are the fused ventral carpellary margins. In the ovule bearing part, ventral parts of carpels have been retracted considerably apparently to accommodate the ovules developing inside.

In the organization of syncarpous ovary from simple carpels in Saururaceae, the so-called classical "torus" is not involved. The evolutionary trend of specialization from laminar to parietal placentation involves: firstly, the fusion of ventral margins of adjacent carpels; and secondly, lateral concrescence of the same carpels. These are further influenced greatly by the ovule bearing capacity of a syncarpous ovary. In *Houttuynia* and *Anemopsis* the ovary becomes "multilocular". The

retraction of partitions within the ovary in the lower part may be due to the acquisition of ovule-bearing capacity of ovary. Normally, the ovaries of genera mentioned above show multilocular nature in the upper part of ovary and unilocular in the lower part. Intermediate conditions showing various stages of phylogenetic retraction of partitions are not infrequent.

Eichler (1875-78) interpreted the flowers of *Saururus* and *Houttuynia* as obdiplostemonous; flowers which had two whorls of three stamens each and the outer whorl had aborted. In the present investigation the above-said feature has not been observed. In *Anemopsis* and *Gymnotheca*, each flower is usually associated with six stamens. Anatomy of flower has shown that traces for stamens arise from the dorsal bundle of carpels. In addition to the above feature, the first formed carpels of *Saururus* usually possess two stamens each, the last formed does not develop stamens. The absence of correlation between the number of carpels and stamens, negates the possibility of recognizing two whorls of stamens. A similar view has also been advanced by Nozeran (1955).

In his comparative survey of floral structures Nozeran (1955) writes that "the spike of *Houttuynia* is not entirely an inflorescence and is not still a flower". Furthermore, he hypothesized that the lowermost bracts transform into perianth lobes. He also observed in inflorescence several instances of reduction in number of stamens and carpels. On the basis of above details, he derived the spike of *Houttuynia* from a homogeneous inflorescence which was composed probably of trimerous flowers. In the present investigation, however, all the details given by Nozeran (1955) were not found. There is no doubt that at the tip of the inflorescence, an overy was often borne, but there has not been enough evidence at present to support Nozeran's hypothesis.

Embryological investigations show great similarities among the three species, *Saururus cernuus*, *Houttuynia cordata* and *Anemopsis*. Development of both male and female gametophytes are very similar. During development of female gametophyte the archesporial cell gives rise to parietal cells in *Saururus* and *Anemopsis*. These parietal cells are absent in *Houttuynia*. The development of the female gametophyte in all three species studied conforms to the monosporic type (as here interpreted). Some stages in the development of endosperm were observed in *Houttuynia* and *Saururus cernuus*. In both cases the endosperm is of the cellular type. The above two genera also show endosperm haustoria. The embryo in *S. cernuus* suggests that the first division of the zygote should be transverse. Seeds enclose a massive perisperm and a little endosperm surrounding the small embryo. Similar embryological features have been recorded by Johnson (1900) for *S. cernuus*.

Summary

An account of floral anatomy and embryology suggests that the genera of Saururaceae are closely interrelated. Structure and morphology of inflorescence and flower are discussed in the light of anatomy.

Anatomical details indicate that the inflorescence-type seen in *Anemopsis* is more specialized than the type seen in *Saururus* or other genera. This has been

achieved, according to the evidences advanced, by processes of reduction, adnation and cohesion of various floral entities.

Some of the morphological aspects of ovary, carpels and placentation have been discussed. Embryological details are similar in all the genera investigated here.

Acknowledgements

I am greatly indebted to Dr. N. H. Nickerson, for his kindness and generosity and valuable guidance during the course of this investigation. I am also highly thankful to Dr. R. E. Woodson, Jr., for generously placing some of the material used here at my disposal and for helpful suggestions.

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HEPATICITES DEVONICUS
A NEW FOSSIL LIVERWORT FROM THE DEVONIAN OF NEW YORK[1,2]

FRANCIS M. HUEBER

ABSTRACT

Hepaticites **devonicus** is described from the lowermost Upper Devonian of New York. Many fragments were obtained by macerating shale This is the oldest fossil hepatic reported to date. It is tentatively considered to be a member of the Anacrogynae, and is compared with the living genera *Pallavicinia* and *Metzgeria*. FRANCIS M. HUEBER, Department of Botany, Cornell University, Ithaca, New York.

INTRODUCTION

The record of the Hepaticae in the Paleozoic is very meager. One may readily expect this to be the case owing to the small size and the delicate nature of the members of this group of plants. Up until now the oldest occurrence of undoubted hepatics was that of four species from the Upper Carboniferous of Shropshire, England (Walton, 1925, 1928). They are *Hepaticites Kidstoni, H. lobatus, H. Langi* (Walton, 1925), and *H. Metzgerioides* (Walton, 1928). These four fossil forms have been compared with the living genera *Treubia, Fossombronia, Riccardia* (*Aneura*) and *Metzgeria* respectively. In all cases the remains are of sterile shoots only and on the basis of their morphology it has been assumed that all of the forms are of the anacrogynous series of the Jungermanniales (Walton, 1925, 571). Definite conclusions can not be made until reproductive organs are found.

MATERIALS AND METHODS

The plant remains which are described here occur as compressions associated with other plant remains in a fine-grained, dark-gray shale. The specimens were collected from a small quarry located on the northwest slope of South Mountain, Schoharie County, New York, 1.1 miles west of the Schoharie–Greene County line Livingston 7′ 30″ map at 74° 16′ 30″ E., 42° 23′ 55″ N. and at an elevation of 2180 feet. The horizon at which the quarry is located is very close to the base of the Onteora "red beds" which are the continental equivalent to the lowermost two-thirds of the marine Finger Lakes stage, Senecan series (Frasnian) of central and western New York. The beds are therefore lowermost Upper Devonian.

The plants with which the specimens of *Hepaticites* are associated, that is in the same beds and at the same quarry, are *Psilophyton princeps* Dawson 1871, *Schizopodium* Harris 1929, *Cladoxylon* Unger 1856, *Pseudosporochnus* Potonie and Bernard 1904, *Eospermatopteris* (Dawson) Goldring 1924, *Callixylon* Zalessky 1911, and two new genera all of which are to be described in future papers.

While preparing transfers of other plant remains, thin fragments of plant material were seen in the sludge derived from the dissolution of the shale. The fragments at first were thought to be epidermal layers from plants contained in the shale. However, after they were washed, dehydrated and mounted, they were

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[1] This paper is a part of a thesis presented to the Graduate School of Cornell University in partial fulfillment of the requirements for the Ph.D. degree.

[2] Communicated by Henry N. Andrews.

found to possess the characteristics of the genus *Hepaticites*. Additional preparations were made using the bulk maceration technique (Harris, 1926). Pieces of rock in which large quantities of plant remains are evident are placed into polyethylene or polystyrene plastic containers. Concentrated hydrofluoric acid (48%) is poured over the specimens until they are completely immersed in the acid. From ten to twenty-four hours are generally required for dissolution of the rock; the time is of course dependent upon the size of the specimen being dissolved. Frequent observations of the progress of the reaction are necessary in order that any freed plant material which is either floating on the surface of the acid or lying in the sludge can be removed. The remains are easily removed by slipping a flat, wooden rod under the specimen and then carefully raising the rod out of the solution. The specimen is "floated" onto the rod in the way that one floats specimens of algae onto paper for the preparation of herbarium sheets. The writer has found that the wooden labels used for flower pots are very satisfactory for lifting the specimens from the solution. The plant material is floated off of the rod into a container of water and washed through three or four changes of water. The wash water is either decanted or siphoned off. After the specimen is washed, it is floated onto a glass slide and positioned on the slide by the use of brushes cut down to a single bristle. The slide is gradually raised from the water, keeping the slide inclined. A drop or two of liquid detergent added to the water will help reduce surface tension and facilitate the removal of the specimen. Any water remaining on the slide and around the specimen is carefully removed with blotting paper. After the specimen has partially dried, it is saturated with a 1% aqueous solution of gum arabic which when dried serves to hold the specimen in place on the surface of the slide. The gum arabic solution is applied with a fine-tipped brush. When the specimen is fully dried, a drop of Harleco Synthetic Mounting Medium or Canada balsam dissolved in xylene is placed on top of it and a coverslip lowered over the surface. At this point, if the specimen were not fixed to the surface of the slide with gum arabic, it would migrate to the edge of the coverslip or be broken by the flow of the viscous mounting medium. The mounting medium is dried and the preparation is ready for study. Nearly eighty fragments were prepared in this way.

Genus HEPATICITES Walton 1925

Hepaticites devonicus sp. nov.—Description

The thallus is very simply differentiated into two parts, a rhizomatous portion and a thallose region. The latter is differentiated into two parts, an axial or costal region composed of elongate parenchymatous cells and marginal wings or lamellae composed of polygonal parenchymatous cells (figs. 1–5). The axial region averages 0.56 mm. in width. It is two to several cells thick; the actual number is impossible to determine because of the complex reticulum formed by the outlines of the cells. A midrib composed of very elongate cells and averaging 0.22 mm. in width forms the central portion of the axial region. The midrib is in turn surrounded by a zone of elongate cells which are transitional in size between the midrib and the cells of the wings. The cells are elongate parallel to the long axis of the thallus and are 14 to 26 μ in diameter. Because of the incomplete preserva-

tion of the end walls, the full length of any one of the cells of the midrib is unknown. The cells which form the transition zone between the midrib and the wings average 140 μ in length. No rhizoids are evident along the axial region. The wings are only one cell thick and vary from 1.3 to 1.75 mm. in width. The cells are 46.8 to 73.2 μ in diameter and are polygonal in outline. Scattered through the tissue of the wings are dark cells (fig. 5). The contents may indicate that some of them were storage or secretory cells. Some, however, may be darkened due to the activity of fungi, for fungal hyphae are commonly observed adhering to the surfaces of the thallus. The margins of the wings are serrate, the teeth are spaced at intervals of 0.18 mm. (figs. 6, 7), but otherwise the margins show no well pronounced lobing. Dichotomous branching of the thallus is evidenced in three specimens, two of which are illustrated in figs. 2 and 3. Fragments of the wings are still attached to the axial regions beyond the dichotomy. Growth of the plant was apparently the result of the divisions of a single apical cell borne in a notch at the apex of the thallus. A fragment of the thallus illustrating what may be interpreted as an example of the apical notch is shown in fig. 4.

The rhizomatous portion of the plant (fig. 8) varies from 0.58 to 1.7 mm. in width and is composed wholly of elongate parenchymatous cells. The midrib varies from 0.15 to 0.28 mm. in width; the cells of which it is composed vary from 14 to 29 μ in diameter and as in the midrib of the thallus portion their length is unknown. The cells which surround the midrib are approximately the same diameter as those in the midrib and they vary from 136 to 220 μ in length. Numerous rhizoids arise from the cells on the surface of the rhizome (figs. 8 and 9). They are nonseptate and average 21 μ in diameter just above the broadened base. The tips of the rhizoids are broken off and therefore the full length of any one individual is not known. The largest fragment is 0.56 mm. in length. It must be stated here that no rhizomatous portion has been found in direct organic connection with the thallose portion of the plant. Both parts were isolated from the same matrix and since the part which is here referred to as the rhizome has the same general form and structure of the axial region of the thallose segment, the writer feels justified in considering them parts of the same plant.

Discussion

A comparsion of the illustrations of *Hepaticites devonicus* with those for the species *H. Metzgerioides* (Walton, 1928, Plate XII, Figs. 1–6) will show how similar the thallose portion of *H. devonicus* is to one which has already been included in the genus *Hepaticites*. The finely serrate margin, the lack of rhizoids on the thallose portion of the plant, and the differentiation of a rhizome bearing rhizoids, all characteristics of *H. devonicus*, are the evident morphological differences between the two species. The difference in the gross size between the two (*H. devonicus* is perhaps four to five times larger than *H. Metzgerioides*) may be of specific value, but the similar size of the constituent cells in the two plants suggests that the difference is probably one of growth form.

As in *H. Metzgerioides*, *H. devonicus* shows a clear distinction between midrib and wing which is also characteristic of the modern genera *Pallavicinia* Gray, corr. Carruthers and *Metzgeria* Raddi. *Hepaticites devonicus* combines characteristics

of both of the modern genera. It is similar to *Pallavicinia* in the width of the thallus (3 to 4 mm.) and may represent a plant like *Pallavicinia Zollingeri* (Gottsch.) Schiffn. (See Smith, 1938, especially Fig. 32 and Campbell and Williams, 1914, especially Fig. 4) in which there is differentiation of a prostrate portion bearing rhizoids and an erect, branched portion on which rhizoids are not present. The small marginal teeth of the thallus in *H. devonicus* is another character which is shared with *Pallavicinia Zollingeri*. *Hepaticites devonicus* differs from *Pallavicinia* in having a less differentiated central strand and larger central cells in the strand. *Hepaticites devonicus* and *Metzgeria* are similar in their slightly differentiated central strands, in the size of the cells in the central strand, the size of the cells in the wings, and the possibility that the teeth on *H. devonicus* are homologous to the hairs on the margins of the thallus in *Metzgeria*. They differ in that *Metzgeria* is smaller (1 to 2 mm. wide) and bears rhizoids along its midrib. *Hepaticites devonicus* resembles *Metzgeria* in cellular details but resembles *Pallavicinia* in size and form.

Reproductive structures are not known for *H. devonicus* but on the basis of its similarity in habit and the many details of structure which it shares with members of the Anacrogynae the writer suggests that it be classed with this group until such a time as further evidence of its relationship is obtained.

The occurence in Devonian sediments of remains assignable to the genus *Hepaticites* extends the range of the Hepaticae even further back in geologic time, and it emphasizes that this class of plants had evolved to a high order of organization far earlier than heretofore recorded.

HEPATICITES **devonicus** Hueber sp. nov.

Diagnosis: Dichotomously branching thallus differentiated into rhizomatous portion bearing rhizoids and thallose portion composed of axial region averaging 0.56 mm. in diameter and wings one cell in thickness ranging from 1.3 to 1.75 mm. in width. Cells of the axial region elongate, 14 to 26 μ in diameter, length of central cells undetermined, length of transitional cells averaging 140 μ. Cells of the wings polygonal, 46.8 to 73.2 μ in diameter. Margins of wings finely serrate, lobing indefinite. Rhizomatous portion 0.58 to 1.7 mm. in diameter, cells elongate as in axial region of thallose portion, numerous non septate rhizoids averaging 21 μ in diameter borne on surface of rhizome.

Holotype number 23, specimen 1579-294, slides 6–12, paleobotanical collections of the Department of Botany, Cornell University, New York.

Locality: Northwest slope South Mountain, Schoharie County, New York.

Horizon: Base of the Onteora "red beds" lowermost Upper Devonian.

SUMMARY

A new species of *Hepaticites, H. devonicus,* is described from the lowermost Upper Devonian of New York. The plant is differentiated into two parts, a rhizomatous portion and a thallose region. The latter is differentiated into two parts, an axial region composed of elongate parenchymatous cells and marginal wings which are one cell thick and composed of polygonal parenchymatous cells.

The margins of the wings are finely serrate and show no lobing. There are no rhizoids borne on the thallose portion of the plant. The rhizome is composed wholly of elongate parenchymatous cells and resembles the axial region of the thallose portion of the plant. Rhizoids occur over the entire surface of the rhizome. No reproductive structures are known.

The plant is compared with *Pallavicinia Zollingeri* and *Metzgeria* and placed for the time being with the fossil forms of the Anacrogynae.

The report constitutes the earliest record of the Hepaticae in the geologic column.

Acknowledgements

The writer wishes to express his sincere appreciation to Dr. Harlan P. Banks for his supervision and guidance during the course of the research which resulted in the discovery of a diverse flora in the Devonian of eastern New York. Special acknowledgement is extended to the National Science Foundation for the support afforded by graduate fellowships for the years 1957-1958, 1958-1959 and 1959-1960 during which time the research was carried to completion. Thanks are extended to Dr. Rudolph Schuster for his suggestions concerning the specimens of *Hepaticites* and to Mrs. J. Douglas Grierson for the photographic prints used to illustrate the present paper.

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EXPLANATION OF PLATE

PLATE I

Hepaticites devonicus

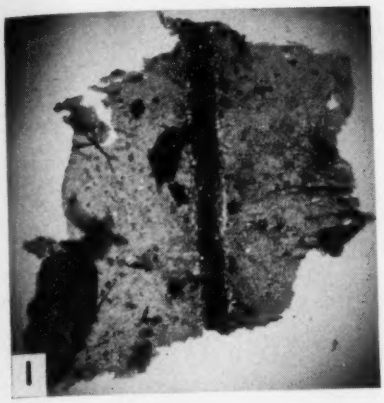
Fig. 1. Portion of the thallose region of the plant showing the differentiation of the axial region and the marginal wings. Slide 12, × 9.

Fig. 2. Portion of the thallose region of the plant showing a dichotomy of the axis. Note the elongate cells of the axial region and the polygonal cells of the marginal wings. Slide 8, × 29.

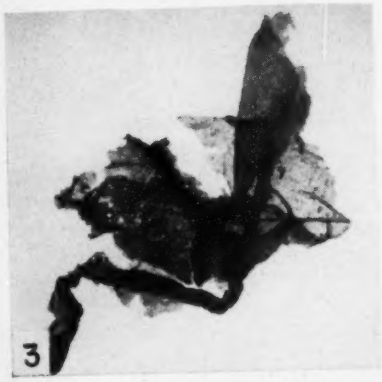
Fig. 3. Portion of the thallose region of the plant showing a dichotomy of the axis. The marginal wings are folded over the midrib in upper portions of the specimen. Slide 9, × 7.

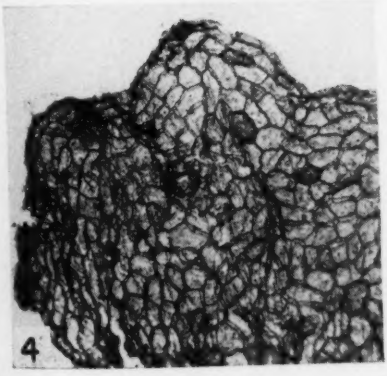
Fig. 4. Apex of the thallose portion of the plant. Slide 11, × 58.

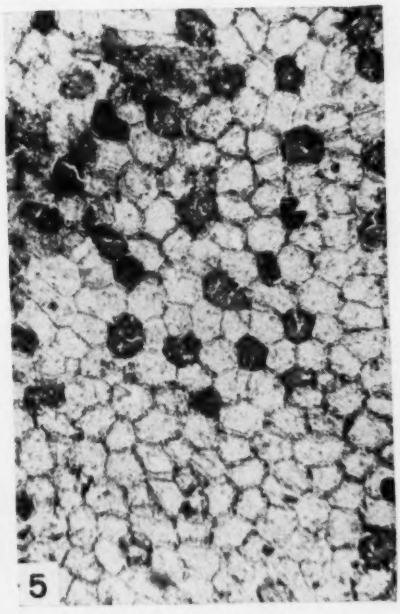
Fig. 5. Detail of the marginal wing of the thallose portion of the plant. Note the darkened cells which may have been storage or secretory cells. Slide 10, × 78.



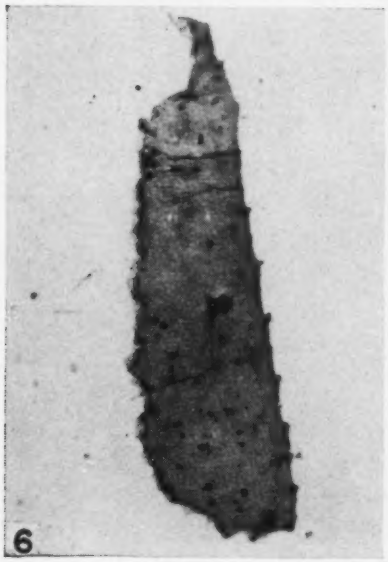




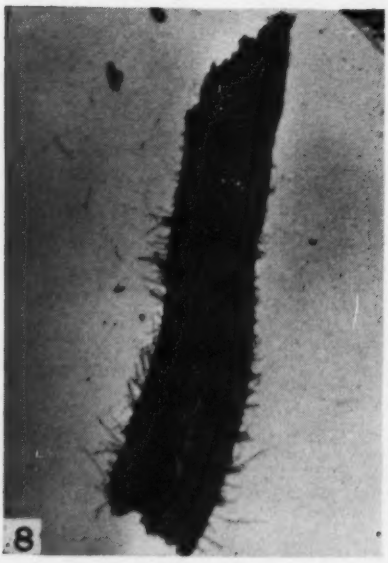




HUEBER—HEPATICITES DEVONICUS









HUEBER—HEPATICITES DEVONICUS

Explanation of Plate

PLATE II

Hepaticites devonicus

Fig. 6. Portion of the marginal wing of the thallose region of the plant illustrating the serrate margin of the wing. Slide 7, × 27.

Fig. 7. Detail of one of the marginal teeth shown on the specimen in Fig. 6. Slide 7, × 205.

Fig. 8. Fragment of the rhizomatous portion of the plant. Note the dense covering of nonseptate rhizoids. Slide 6, × 16.

Fig. 9. Detail of the surface of the rhizomatous portion of the plant showing the broad bases of the rhizoids. The tips of the rhizoids are broken off. Slide 6, × 190.

INDEX OF ORCHID NAMES — 1960

ROBERT L. DRESSLER

As an aid to ourselves and others studying the orchids, we have started an index of new orchid names, to be published annually. It is felt that such an index may be of value to the many botanists and others interested in this large and complex family. For new taxa we have indicated the country or origin and the location of type material (using the standard abbreviations), if this is known. For new combinations, new names or changes in rank, we cite the basionym with the new name. We have abbreviated the authors' names less than is customary, as we feel that a saving of only one or two spaces does not justify the loss of clarity. A few names which were published in mimeographed news letters are purposely omitted. Such publication is of dubious validity under the rules of nomenclature, and certainly should be avoided. We would be very glad to receive corrections or additions to the index, to be appended to the Index for 1961.

Subfamily **Cypripedioideae** Garay, Bot. Mus. Leafl. 19:86. Type genus: *Cypripedium* L.

Subfamily **Epidendroideae** Dressler, Taxon 9:213. Based on *Kerosphaeroideae* Garay.

Subfamily **Kerosphaeroideae** Garay, Bot. Mus. Leafl. 19:87. Type genus: *Epidendrum* L. This name is not legitimate under the Rules of Nomenclature.

Subfamily **Neottioideae** Garay, Bot. Mus. Leafl. 19:86. Type genus: *Neottia* Sw.

Subfamily **Ophrydoideae** Garay, Bot. Mus. Leafl. 19:87. Type genus: *Orchis* L. This name is not legitimate under the Rules of Nomenclature; this subfamily must be known as the Orchidoideae.

Aeranthes **albidiflora** Toilliez-Genoud, Ursch & Bosser, Not. Syst. Paris 16: 205. Madagascar (TAN).

Aeranthes **ambrensis** Toilliez-Genoud, Ursch & Bosser, Not. Syst. Paris 16: 209. Madagascar (TAN).

Aeranthes **carnosa** Toilliez-Genoud, Ursch & Bosser, Not. Syst. Paris 16: 209. Madagascar (TAN).

Aeranthes **denticulata** Toilliez-Genoud, Ursch & Bosser, Not. Syst. Paris 16: 207. Madagascar (TAN).

Aeranthes **neoperrieri** Toilliez-Genoud, Ursch & Bosser, Not. Syst. Paris 16: 212. Madagascar (TAN).

Aeranthes **orthopoda** Toilliez-Genoud, Ursch & Bosser, Not. Syst. Paris 16: 212: Madagascar (TAN).

Bletia purpurea var. **alba** Ariza-Julia & Jiménez, Rhodora 62:236. Dominican Republic.

Bulbophyllum jacquetii var. **rosea** Guillaumin, Bull. Mus. Hist. Nat. Paris II 32: 189. Annam (P?).

Bulbophyllum **rugosibulbum** Summerh., Kew Bull. 14:138. Northern Rhodesia (K).

Cephalantheropsis lateriscapa Guillaumin, Bull. Mus. Hist. Nat. Paris II 32: 188–189. Annam (P?).

Chroniochilus **virescens** (Ridley) Holttum, Kew Bull. 14:273. *Sarcochilus virescens* Ridley.

Cleisostoma **tixieri** Guillaumin, Bull. Mus. Hist. Nat. Paris II 32:369. Annam (P?).

Cypripedium × *andrewsii* nm. **favillianum** (J. T. Curtis) Boivin, Naturaliste Canadien 87:32. *Cypripedium* × *favillianum* J. T. Curtis.

Cypripedium × *andrewsii* nm. **landonii** (Garay) Boivin, Naturaliste Canadien 87: 32. *Cypripedium* × *landonii* Garay.

Cyrtorchis arcuata ssp. **leonensis** Summerh., Kew Bull. 14:149. Sierra Leone (K).

Cyrtorchis arcuata ssp. **variabilis** Summerh., Kew Bull. 14:148. Tanganyika Terr. (K).

Cyrtorchis arcuata ssp. **whytei** (Rolfe) Summerh., Kew Bull 14:147. *Listrostachys whytei* Rolfe.

Cyrtorchis **neglecta** Summerh., Kew Bull. 14:149. Tanganyika Terr. (K.)

Dactylorhiza—Soó (Ann. Univ. Scient. Budapest. Eötvös Biol. 3:335–357) gives a synopsis of *Dactylorhiza* (*Dactylorchis*) which includes many apparent new combinations for species, subspecies and hybrid populations. We do not list these here because there is not "a full and direct reference to its author and original publication" with the basionyms. Further, it is quite unclear just which names Soó intends to publish as new combinations. It seems unlikely that one would intentionally publish so many new combinations in *Dactylorhiza* while recommending that *Dactylorchis* be considered for conservation.

Diaphananthe section **Rhipidoglossum** (Schltr.) Summerh., Kew Bull. 14:141. *Rhipidoglossum* Schltr.

Diaphananthe **brevifolia** (Summerh.) Summerh., Kew Bull. 14:143. *Rhipidoglossum brevifolium* Summerh.

Diaphananthe **cuneata** Summerh., Kew Bull. 14:141. Uganda (K).

Diaphananthe **densiflora** (Summerh.) Summerh., Kew Bull. 14:143. *Rhipidoglossum densiflorum* Summerh.

Diaphananthe **erecto-calcarata** (De Wild.) Summerh., Kew Bull. 14:143. *Angraecum erecto-calcaratum* De Wild.

Diaphananthe **globoso-calcarata** (De Wild.) Summerh., Kew Bull. 14:142. *Angraecum globoso-calcaratum* De Wild.

Diaphananthe **laxiflora** (Summerh.) Summerh., Kew Bull. 14:141. *Rhipidoglossum laxiflorum* Summerh.

Diaphananthe **longicalcar** (Summerh.) Summerh., Kew Bull. 14:142. *Rhipidoglossum longicalcar* Summerh.

Diaphananthe **microphylla** (Summerh.) Summerh., Kew Bull. 14:142. *Rhipidoglossum microphyllum* Summerh.

Diaphananthe **obanensis** (Rendle) Summerh., Kew Bull. 14:142. *Angraecum obanense* Rendle.

Diaphananthe **peglerae** (Bolus) Summerh., Kew Bull. 14:143. *Mystacidium peglerae* Bolus.

Diaphananthe **rohrii** (Reichb. f.) Summerh., Kew Bull. 14:140. *Angraecum rohrii* Reichb. f.

Diaphananthe **rutila** (Reichb. f.) Summerh., Kew Bull. 14:143. *Aëranthus rutilus* Reichb. f.

Diaphananthe **xanthopollinia** (Reichb. f.) Summerh., Kew Bull. 14:143. *Aëranthus xanthopollinius* Reichb. f.

Dinklageëlla **minor** Summerh., Kew Bull. 14:156. Liberia (K).

Epidendrum **hioramii** Acuña & Alain, Mem. Soc. Cubana Hist. Nat. 24:110. Cuba (SV).

Epipactis thunbergii forma **subconformis** Sakata, Jour. Jap. Bot. 35:224. Japan (Herb. T. Sakata).

Eulophia **laurentii** (De Wild.) Summerh., Kew Bull. 14:139. *Lissochilus laurentii* De Wild.

Habenaria section **Kryptostoma** Summerh., Kew Bull. 14:135. Type species: *H. tentaculigera* Reichb. f.

Habenaria **gonatosiphon** Summerh., Kew Bull. 14:134. Tanganyika Terr. (K).

Habenaria **magnirostris** Summerh., Kew Bull. 14:132. Tanganyika Terr. (K).

Habenaria **richardsiae** Summerh., Kew Bull. 14:131. Tanganyika Terr. (K).

Holothrix **brachycheira** Summerh., Kew Bull. 14:127. Northern Rhodesia (K).

Holothrix **papillosa** Summerh., Kew Bull. 14:128. Tanganyika Terr. (K).

Holothrix **pentadactyla** (Summerh.) Summerh., Kew Bull. 14:129. *Deroemera pentadactyla* Summerh.

Laeliopsis domingensis var. **alba** Ariza-Julia & Jiménez, Rhodora 62:236. Dominican Republic.

Luisia **acutilabris** Guillaumin, Bull. Mus. Hist. Nat. Paris II 32:188. Laos (P?).

Masdevallia **horrida** Teuscher & Garay, Amer. Orchid Soc. Bull. 29:23. Costa Rica (AMES).

Maxillaria imbraicata var. **carinata** (Rodr.) Pabst, Orquidea (Brazil) 22: 134. *Maxillaria carinata* Rodr.

Maxillaria imbricata var. **iguapensis** (Hoehne & Schltr.) Pabst, Orquidea (Brazil) 22: 134. *Maxillaria iguapensis* Hoehne & Schltr.

Oberonia **attenuata** Dockrill, No. Queensland Naturalist 29:4. Australia (BRI).

Oberonia recurva var. **lingmalensis** (Blatt. & McC.) Sant. & Kapadia, Jour. Bombay Nat. Hist. Soc. 57:259. *Oberonia lingmalensis* Blatt. & McC.

Oberonia **santapaui** Kapadia, Jour. Bombay Nat. Hist. Soc. 57:265. *Oberonia lindleyana* Wight, 1851, not O. *lindleyana* Duperr., 1834.

Oberonia **trullaelabris** Guillaumin, Bull. Mus. Hist. Nat. Paris II 32:115. Annam (P?).

Orchis rotundifolia forma **beckettii** Boivin, Naturaliste Canadien 87:42. Canada (DAO).

Peristylus **densus** (Lindley) Santapau & Kapadia, Jour. Bombay Nat. Hist. Soc. 57:128. *Coeloglossum densum* Lindley.

Polystachya **bella** Summerh., Kew Bull. 14:137. Kenya Colony (K).

Polystachya **testuana** Summerh., Kew Bull. 14:136. Gabon (Herb. Le Testu).

Pteroceras **alatum** (Holttum) Holttum, Kew Bull. 14:269. *Sarcochilus alatum* Holttum.

Pteroceras **appendiculatum** (Bl.) Holttum, Kew Bull. 14:269. *Dendrocolla appendiculata* Bl.

Pteroceras **berkeleyi** (Reichb. f.) Holttum, Kew Bull. 14:269. *Thrixspermum berkleyi* Reichb. f.

Pteroceras **biserratum** (Ridley) Holttum, Kew Bull. 14:269. *Sarcochilus biserratus* Ridley.

Pteroceras **caligare** (Ridley) Holttum, Kew Bull. 14:269. *Sarcochilus caligaris* Ridley.

Pteroceras **carrii** (L. Wms.) Holttum, Kew Bull. 14:269. *Sarcochilus carrii* L. Wms.

Pteroceras **ciliatum** (Ridley) Holttum, Kew Bull. 14:269. *Dendrocolla ciliata* Ridley.

Pteroceras **compressum** (Bl.) Holttum, Kew Bull. 14:270. *Dendrocolla compressa* Bl.

Pteroceras **ecalcaratum** (Holttum) Holttum, Kew Bull. 14:270. *Sarcochilus ecalcaratus* Holttum.

Pteroceras **emarginatum** (Bl.) Holttum, Kew Bull. 14:270. *Dendrocolla emarginata* Bl.

Pteroceras **fasciculatum** (Carr) Holttum, Kew Bull. 14:270. *Sarcochilus fasciculatus* Carr.

Pteroceras **hirsutum** (Hooker f.) Holttum, Kew Bull. 14:270. *Sarcochilus hirsutus* Hooker f.

Pteroceras **johorense** (Holttum) Holttum, Kew Bull. 14:270. *Sarcochilus johorensis* Holttum.

Pteroceras **minutiflorum** (Ridley) Holttum, Kew Bull. 14:270. *Asochilus minutiflorus* Ridley.

Pteroceras **pallidum** (Bl.) Holttum, Kew Bull. 14: 270. *Dendrocolla pallida* Bl.

Pteroceras **siamense** (Ridley) Holttum, Kew Bull. 14:271. *Asochilus siamensis* Ridley.

Pteroceras **stenoglottis** (Hooker f.) Holttum, Kew Bull. 14:271. *Sarcochilus stenoglottis* Hooker f.

Pteroceras **sauveolens** (Roxb.) Holttum, Kew Bull. 14:271. *Aërides suaveolens* Roxb.

Pteroceras **tanyphyllum** (Ridley) Holttum, Kew Bull 14:271 *Sarcochilus tanyphyllus* Ridley.

Pteroceras **teres** (Bl.) Holttum, Kew Bull. 14:271. *Dendrocolla teres* Bl.

Pteroceras **teysmannii** (Miq.) Holttum, Kew Bull. 14:271. *Aërides teysmannii* Miq.

Pteroceras **violaceum** (Ridley) Holttum, Kew Bull. 14:272. *Sarcochilus violaceus* Ridley.

Pteroceras **viridiflorum** (Thw.) Holttum, Kew Bull. 14:272. *Aërides viridiflora* Thw.

Pteroceras **zollingeri** (Reichb. f.) Holttum, Kew Bull. 14:272. *Dendrocolla zollingeri* Reichb. f.

Schizochilus **lepidus** Summerh., Kew Bull. 14:130. Mozambique (Southern Rhodesia Gov. Herb.).

Schomburgkia × **parkinsoniana** H. G. Jones, Jour. Barbados Mus. Hist. Soc. 28: 4. Barbados (parent species introduced).

Thrixspermum **pygmaeum** (King & Prantl.) Holttum, Kew Bull. 14:275. *Sarcochilus pygmaeus* King & Prantl.

PRELIMINARY STUDIES IN THE GENUS STANHOPEA (ORCHIDACEAE)

C. H. DODSON AND G. P. FRYMIRE

ABSTRACT

This preliminary study is an attempt to bring together the knowledge of Taxonomy, Morphology, Phylogeny and Pollination of the species preparatory to a formal revision of the genus. New information, gathered by population study in the natural habitats, appears to be highly significant to the understanding of this complex group.

The distribution of the species is mapped. The phylogenetic relationships of the genus are considered and it is believed that *Stanhopea* is derived from plants similar to members of the genus *Sievekingia*. The development of the advanced and complex species from the simpler species is discussed and the origin of certain unique species such as *S. tricornis* is considered.

Observations of pollination of *S. tricornis* by *Eulaema meriana* and of *S. bucephalus* by *Eulaema bomboides* are discussed and pollination relationships are indicated as the major means of genetic isolation of the two species.

Two highly variable populations were studied in Ecuador. The advanced and variable complexes in *Stanhopea* are very successful both in area of range and density of population. It is felt that this population structure suppresses speciation as a process, though variability is maintained.

Various nomenclatural problems are mentioned and a key to the species is included. A list of the recognized species is given with their synonyms, and a list is appended of poorly known species which cannot as yet be properly placed.

CALAWAY H. DODSON, Missouri Botanical Garden, 2315 Tower Grove Ave., St. Louis 10, Missouri.

To say that the genus *Stanhopea* is poorly understood is an understatement. Rather it is in a state of taxonomic chaos. Before we can say that a genus is understood it is expected that an individual plant, taken at random from a population of similar plants, can be fitted into a species concept. That is to say, it should be possible for a trained botanist to determine whether an individual belongs to a known species or is new and unknown. At the present time the only way to deal with most individual plants of this genus is to name them as new species, thus defeating the whole precept of taxonomy. Throughout its range of distribution *Stanhopea* is characterized by populations which are extremely variable. The variability within a single population can be so extreme as to appear as a hybrid swarm in which are represented many kinds of *Stanhopea* hitherto considered as different species.

Because of the plant to plant variability within a single population, a great number of species have been described from single specimens growing in European greenhouses. Often the origin of these plants was not even known. Only the fact that they were different from the other known specimens was taken into consideration and that difference was considered sufficient reason for a new species description. It has been estimated that at least 500 names have been proposed in *Stanhopea* (Ames and Correll, 1953). This estimate is high, actually only slightly over 100 names have been published. Recent works have reduced that number to between 25 and 50 which are considered as even reasonably valid.

One of the problems involved in the classification of this group is that the flowers are large and fleshy and of intricate structure. They do not preserve well as herbarium specimens and many of the structures of the lip in particular are destroyed or altered in drying. The flowers are not long lasting and seldom persist on the plant for more than three or four days. They are therefore difficult to study

in the field since not many flowers can be seen at any one time within a population. Their period of flowering is often extended over a period of from five to seven months and a plant which is not large will generally flower only once in a given year.

Since they are difficult to study in the herbarium it has been suggested that the only way to straighten out the taxonomic confusion in the genus would be by persistent field work. Our work bears out this suggestion and we do not as yet feel qualified to publish a revision of the genus even though we have studied a considerable number of large populations. We have also studied most of the available herbarium material, but find it hopelessly unrewarding. Such large fleshy flowers as are found in this group do not, as a general rule, make good specimens when crushed and dried. Even after boiling, the critical characters are often lost and determination is difficult. Our experience indicates that dried specimens made from the same plants on different occasions are so altered in drying that they can easily be given separate species designations. This situation is particularly true in certain of the critical species groups which are separated on small differences in structure of the fleshy parts of the lip.

Perhaps all is not as hopeless as it appears on the surface. A number of workers have made limited regional studies for orchid floras. A survey of their work reveals that though they do not all agree, they do not seriously disagree in respect to the majority of the species. In fact, some species appear to be remarkably distinct and do not demonstrate significant variation within their populations. Therefore they are given recognition by each of these workers when they occur in regions treated by them.

When the species in which the problems occur are separated from the ones which are distinct we find that the latter group is not a difficult one. Each species has a distinct distribution and to a certain degree a distinct habitat. Within the problem group the species vary tremendously yet they are in many respects remarkably alike, particularly in morphological characteristics. We feel that this is the key to the problem. They are not only remarkably alike, they *are* alike and only represent variations of a pattern If these complexes were treated as representing fewer species each of which may vary considerably within a particular population, then the genus probably could be treated taxonomically and could be understood.

Morphology

Let us consider just what combination of characteristics place a plant in the genus *Stanhopea*. The vegetative characters are surprisingly uniform, so much so that it is nearly impossible to distinguish species without flowers. All are epiphytic or lithophytic. The pseudobulbs are usually large, ovoid, ribbed and unifoliate. The leaves are broad, elliptic-lanceolate, contracted into a petiole at the base and are strongly veined and plicate. The inflorescence consists of a short pendulous raceme with several broad, papery bracts. The flowers are large, long pedicellate and shielded by a papery bract, this often brightly colored and generally similar in aspect to the sepals and petals. Nearly all species produce a strong fragrance, some being agreeable and others not. The sepals are membranaceous and concave, the dorsal sepal is free and erect and the lateral sepals broad, reflexed and connate at



Fig. 1. Distribution of the genus Stanhopea.

the base. The petals in most species are membranaceous, subequal to the dorsal sepal and recurved. The principal characters which separate the species are to be found in the labellum. In general, the lip consists of three parts: the hypochile or globular, concave part nearest the base of the flowers; the mesochile, which is short and often projected on each side to form horns; and the articulated epichile, which is variously shaped but usually ovate. Certain of the species, such as S. *ecornuta* Lehm. and S. *pulla* Rchb. f., simply have a saccate, entire lip which would correspond to the hypocile of the more complex forms. These should perhaps be considered as the more primitive forms and later discussion will attempt to show why. The column is rather similar in most of the species and is elongate and rather slender with or without broad lateral wings. The anther is ventral, incumbent and two-celled. The pollen apparatus consists of a lanceolate viscidium which rests on an elongate spine-like rostellum, a stipe which is long and narrow, and the two pollinia which are elongate, quite thin, and recurved. The stigma forms a pocket under the rostellum.

Distribution

The genus is distributed from central Mexico through Central America and most of northern South America into southern Brazil The plants are generally found in localities where at least some shade is afforded and where they will rarely

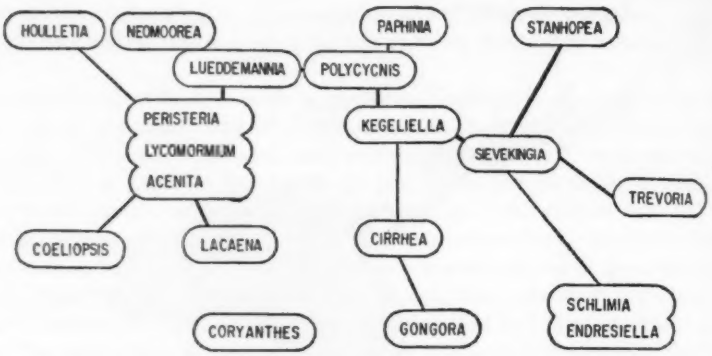


Fig. 2. A diagram of suggested generic relationships within the tribe Stanhopeinae.

become dry. They can withstand prolonged periods of moderate drouth but need considerable water during their growing season.

Figure 1 shows the distribution of the genus. *Stanhopea lewisae* Ames & Correll occurs in Guatemala and Costa Rica. *Stanhopea ecornuta* Lindl. occurs in Honduras, Guatemala, Nicaragua and Costa Rica and S. *cirrhata* Lindl. is found in Nicaragua and Costa Rica. *Stanhopea pulla* Rchb. f. is found in Costa Rica and Panama. *Stanhopea grandiflora* Lindl.* extends from Trinidad through Venezuela, northern Brazil and the Amazon drainage region of Colombia, Ecuador and Peru. *Stanhopea rodigasiana* Hort. and S. *reichenbachiana* Roezl. ex Rchb. f. are little known species which occur in Colombia. *Stanhopea connata* Kl. occurs in eastern Ecuador and Peru and S. *tricornis* Lindl. is restricted to coastal Ecuador and southern Colombia. The remaining species in the genus fall into two major complexes. The first of these groups include S. *insignis* Frost, S. *tigrina* Batem., S. *martiana* Batem. ex Lindl. and S. *saccata* Lindl. The second group is composed of S. *oculata* Lindl., S. *bucephalus* Lindl., S. *wardii*. Lodd. ex Lindl., and a considerable number of lesser known forms which are quite similar. These two groups occur throughout the range of the genus from Mexico to southern Brazil; however, certain forms are restricted to geographic regions.

Phylogeny

The genus *Stanhopea* was taken by Bentham (1881) as the type of the subtribe and thus the name Stanhopeinae should be used in place of Gongorinae Schltr. (See Dressler and Dodson, 1960). As close allies *Stanhopea* has the following genera: *Sievekingia, Polycycnis, Paphinia, Cirrhea* and *Gongora* and perhaps *Peristeria* and *Houlletia*. All of the species within these genera have a labellum which is more

*See the section on Taxonomy for the reason for using this name in place of the commonly used S. *eburnea* Lindl.

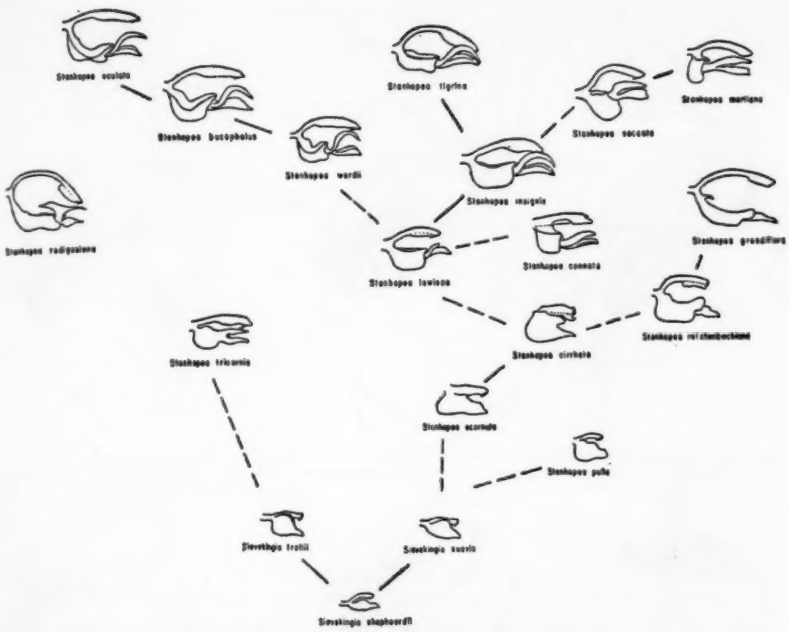


Fig. 3. A diagram of the lip and column of the members of *Stanhopea* and the closely allied species of *Sievekingia* suggesting relationships between the species. Solid lines represent close relationships, while dashed lines represent relationships which are more distant or less clear.

or less divided into a hypochile and an epichile. Figure 2 illustrates a possible phylogenetic series demonstrating the relationships of the genera within the Stanhopeinae.

We do not feel that a discussion of the phylogenetic relationships of the other members of the Stanhopeinae would fall within the purpose of this paper and therefore will only discuss those genera which seem to be directly involved with *Stanhopea* in a stepwise progression from the simple to the complex. The genera placed at the center of the diagram in Figure 2 have a rather simple labellum and as the list radiates outward toward the more advanced genera the lip becomes more complicated.

Figure 3 demonstrates our concepts of the origin and development of the Stanhopeas from the poorly known genus *Sievekingia*, a genus of about seven species. In general the plants are very similar to small immature Stanhopeas and for this reason are often neglected by collectors. Very few specimens of these plants are in herbaria and in several instances the type is the only specimen in existence. Members of this genus were not discovered until late in the 19th Century and thus did not receive so many generic names as some of the earlier discovered members of the subtribe. Without doubt certain of the species placed in *Sievekingia* show fewer morphological relationships to each other than do the following genera to each other: *Acineta*, *Lycomormium*, *Peristeria*, *Coeliopsis*,

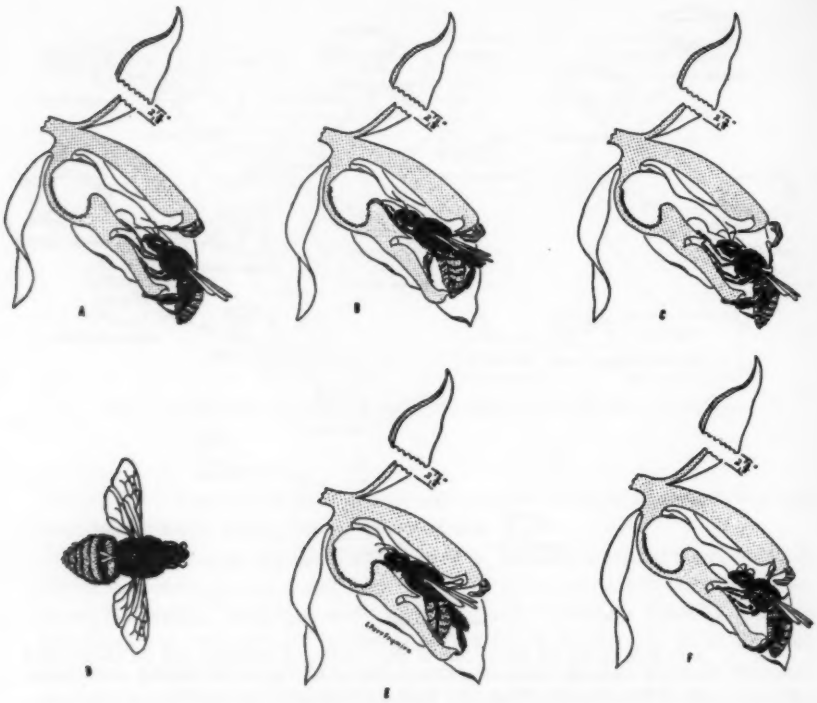


Fig. 4. A diagrammatic representation of the pollination of *Stanhopea tricornis* Lindl. by *Eulaema meriana* A. Bee entering the flower. B. Bee backing out of the flower with the spine of the rostellum engaged under the metathorax. C. Bee leaving the flower with the viscidium attached to the metathorax. D. Bee in flight with the pollinarium in place. E. Bee after entering another flower, showing the pollinia inserted in the stigmatic cleft. F. Bee leaving the 2nd flower, showing the pollinia left in the stigmatic cleft.

Neomoorea, Lacaena and *Lueddemania.* The flowers of the Sievekingias are for the most part less complex than the Stanhopeas. *Sievekingia shepheardii* Rolfe has a semierect inflorescence with rather simple flowers which have only a slightly lobed, truncate lip with a simple fimbriate callus in the center. This is certainly the most primitive known species at least in respect to the labellum. *Sievekingia suavis* Rchb. f. and *S. peruviana* Rolfe have somewhat larger, erect side lobes which form a concave hypochile at the base of the lip. From this point the close relationships of the more primitive Stanhopeas are obvious. It is a simple step from *Sievekingia* to *Stanhopea ecornuta* and *S. pulla* in which the lip is saccate and without the complicated mesochile and epichile of the more advanced Stanhopeas.

Stanhopea cirrhata (Fig. 8) is probably an advancement from a plant similar to *S. ecornuta* (Fig. 6) or *S. pulla* (Fig. 7) through the development of lobes along the upper edge of the hypochile. In other respects *S. cirrhata* is rather similar to the two primitive species except for the narrow, caudate wings formed along each

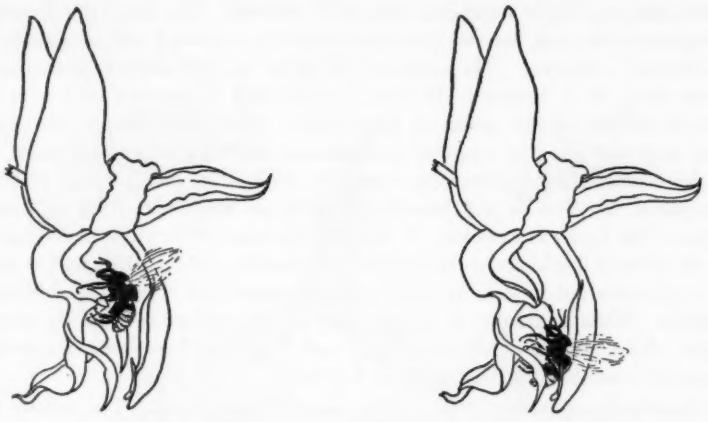


Fig 5. A diagrammatic representation of the pollination of *Stanhopea bucephalus* Lindl. by *Eulaema bomboides* Friese. A. Bee attempting to land on the waxy surface of the hypochile. B. Bee falling down through the flower.

side of the column. This may be the basic form from which the two major branches of *Stanhopea* have developed. On one side, S. *reichenbachiana* (Fig. 10) could have been derived from S. *cirrhata* and could well have been the form from which *Stanhopea grandiflora* (Fig. 11) developed. *Stanhopea grandiflora* has a fairly complex lip with short horns produced from the hypochile rather than from the mesochile as in many species.

Stanhopea cirrhata could also be considered as similar to the ancestral form from which S. *lewisae* (Fig. 13) developed. *Stanhopea lewisae* has very small, slightly developed horns on the mesochile. Most of the advanced species with well developed horns on the mesochile may well have been derived from S. *lewisae* or a similar form.

Stanhopea tricornis (Fig. 9) shows little relationship to the other species in the genus. The petals are thick and fleshy and are held parallel to the lip and column. The lip has a hypochile which is only slightly saccate, no true mesochile and a very thick and fleshy epichile. The horns are produced as an extension of the hypochile and a sharp spine-like callus forms a third horn between the two lateral horns in the place of a mesochile. Two possibilities can be postulated for the origin of this unique species. First, it could have developed through evolution from the other known species of primitive *Stanhopea* as an isolated form. No intermediates are known, however, between this species and the other known Stanhopeas. The second hypothesis may seem a bit far-fetched, but there is some morphological evidence for derivation of S. *tricornis* from a species of *Sievekingia*, S. *trollii* Mansf., recently encountered as sympatric with this *Stanhopea*. This *Sievekingia* has petals similar to S. *tricornis*. The plant is so similar that it doubtless has been passed over by previous collectors (including ourselves) as a young *Stanhopea*. A colored slide taken of this species, without a scale to indicate size, was at first

determined as a highly floriferous form of S. *tricornis*. The lip of this *Sievekingia* is saccate at the base, has two side lobes which flare outward and an epichile very similar to S. *tricornis*. The callus of the lip is in some respects similar to the center horn of S. *tricornis*. It seems feasible that S. *tricornis* may have been derived by way of this species of *Sievekingia*. *Stanhopea tricornis* may possibly have been derived as a result of hybridization between *Sievekingia trollii* or a similar form and some *Stanhopea* sympatric with it in distribution. *Stanhopea bucephalus*, S. *tricornis* and *Sievekingia trollii* are sympatric along the western slopes of the Andes in Ecuador. If chance pollination of *Stanhopea bucephalus* by the *Sievekingia* should occur the resulting intermediate hybrid might well be visited by a pollinator not utilized by either parental species and thereby be stabilized as a species. When an attempt is made to draw an intermediate between the morphological characteristics of the *Sievekingia* and *Stanhopea bucephalus* the result is surprisingly similar to the labellum of S. *tricornis*.

Stanhopea rodigasiana (Fig. 12) is unique in the genus. The strictly one-flowered inflorescence, ovoid, smooth pseudobulbs, bifid rostellum, round viscidium and unique horns on the lip are characters not found in any other *Stanhopea*. In some respects it suggests a possible relationship to *Paphinia*, but it is certainly close to *Stanhopea*. It is surprising to us that this species was never placed in a monotypic genus. Although it is obviously closely related to *Stanhopea* it is sufficiently different from the other species in the genus to allow any taxonomist with a narrow generic concept to separate it without qualms of conscience. The reason for its not having been so separated is very likely that it was not discovered until after the turn of the century, when more care was being taken in such matters. If it had been discovered 50 years earlier when *Peristeria*, *Acineta*, *Lycomormium*, and other closely allied genera, were being separated, it would surely have been considered as generically distinct. We do not believe that it warrants special distinction nor do we believe that so many genera should be recognized in the *Peristeria* complex. We hope that through more careful study of the entire subtribe Stanhopeinae we will be able to develop a useful revision of its members.

The above mentioned species of *Stanhopea* are for the most part easily recognized, have distinct morphological characters and distributional patterns. They present no serious problems to the taxonomist. The remaining species within the genus form the difficult portion. All of them have a more complex labellum than the species previously discussed. The hypochile is saccate and of various sizes but it follows a similar pattern in all of the species. The mesochile is short and inserted on the apex of the hypochile with two lateral, elongate horns of various sizes. The epichile is articulated to the apex of the mesochile and while it may vary in size and proportions, they are all similar. Two major groups can be separated and while we are not yet prepared to present a formal revision of the genus we feel that some designation is necessary in order to be able to group the excessively large number of species names in such a way that they can be discussed with relative ease. We will use the terms "*oculata* complex" for those plants similar to S. *oculata*, and "*insignis* complex" for the plants allied to S. *insignis*. The "*oculata* complex" will therefore comprise those concepts which have a rather long narrow or rectangular



Fig. 6. *Stanhopea ecornuta* Lem. A. Inflorescence (× ⅓). B. Plant habit (× 1/9). C. Side view of the lip and column (× ½). D. Dorsal view of the lip (× 1). E. Pollinarium (× 3).

hypochile, large mesochile horns and always have an entire, acute or apiculate epichile. The "*oculata* complex" comprises such taxa as: *S. wardii* Lodd. ex Lindl., (Fig. 21), *S. oculata* (Lodd.) Lindl. (Fig. 19), *S. bucephalus* Lindl, (Fig. 20), *S. haseloviana* Rchb. f., *S. platyceras* Rchb. f., etc. The "insignis complex" will consist of those forms which have a saccate or globular hypochile, large mesochile horns and either entire, acute or three-lobed epichiles. The "*insignis* complex" comprises such species as *S. tigrina* Batem. ex Lindl. (Fig. 16), *S. martiana* Batem. ex Lindl. (Fig. 17), *S. insignis* Frost (Fig. 15), *S. saccata Batem.* (Fig. 18) and *S. devoniensis* Lindl.

Stanhopea quadricornis Lindl., if such a species exists, has a lip which is within the variation pattern of *S. oculata* with the exception that the base of the thickenings of the margin of the hypochile are projected into short horns. Apparently only one specimen was collected and was named by Lindley. It is quite possible that it was only an aberrant specimen or a hybrid and was not representative of any population.

It seems apparent that *Stanhopea* is a rather terminal group in evolution, with *Coryanthes*, a genus often said to be closely allied to *Stanhopea*, having a derivation

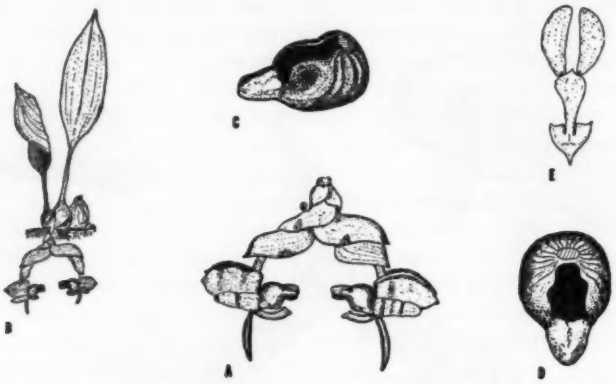


Fig. 7. *Stanhopea pulla* Rchb. f. A. Inflorescence (× ⅓). B. Plant habit (× 1/12). C. Side view of the lip (× 1). D. Dorsal view of the lip (× 1). E. Pollinarium (× 3).

from some similar ancestor, but one probably more closely allied to *Peristeria* than to *Stanhopea*. *Cirrhea* and *Gongora* appear to be the termination of a separate line.

In general, the Orchidaceae appears to be a rather recent but rapidly evolving family in which less extinction is evident than in older families. Such a situation often makes classification difficult due to the intergrading forms, but on the other hand, it makes the tracing of phylogeny easier since closely related groups are still present. We do feel that the Stanhopeas were derived from ancestors very much like some of the species of *Sievekingia* which are known today. The species of *Sievekingia* are not particularly successful, as is evident from their extreme rarity, but may be considered as relict forms locally preserved in relatively hospitable habitats. Such forms would very likely become extinct and be removed from the record if they were members of plant families subjected to more stringent environmental conditions.

POLLINATION

This paper is perhaps somewhat premature in one respect, that is, the pollinators and pollination mechanisms are not as yet known for all the species. However it may be many years before all the information can be gathered. We feel that the major worth of the paper lies in its discussion of the problems within the genus.

The pollination mechanisms and pollinators of two species have been well worked out and photographed. Pollination studies of the other species will be described when they are known. We have witnessed the pollination of both *Stanhopea tricornis* and *S. bucephalus* in Ecuador.

A future revision of this genus may well be based in large part upon the ideas gained from observations of pollination. Polymorphic genera are often difficult to understand and when confusion is compounded by having highly variable populations, the naming of which has been multiplied on an unrealistic basis, such a genus

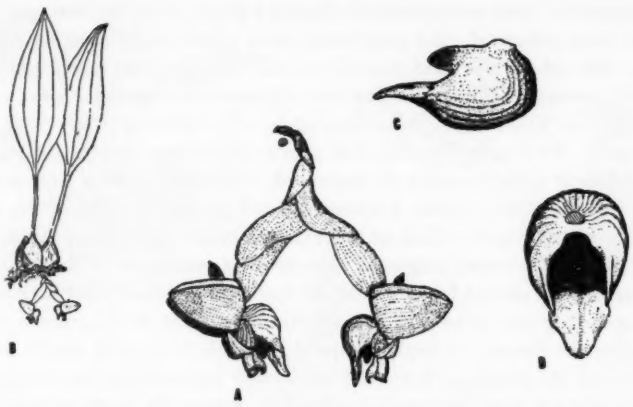


Fig. 8. *Stanhopea cirrhata* Lindl. A. Inflorescence (× ⅓). B. Plant habit (× 1/17). C. Side view of the lip (X ⅔). D. Dorsal view of the lip (× ⅔).

becomes chaotic. Occasionally new techniques or observations from a different standpoint, can provide flashes of insight for the investigator. The totally different pollination mechanisms of these kinds of Stanhopeas, when observed, immediately and clearly made obvious certain of the reasons for the polymorphism within the genus. The first system is typical of most orchids in which the pollinator simply enters the flower after landing on the expanded labellum. The transfer of pollinia occurs as a result of proper positioning of the column and its sexual apparatus in relation to the size and conformity of the particular pollinator. The majority of the species of *Stanhopea* are of this type. These species are not extremely variable and are easily recognized.

The second is a highly complex system in which the flight characteristics of the bee are used in the pollination of the flower. After landing, the bee is clumsy and has difficulty in regaining balance in flight. The bee, unable to grasp the slick surfaces of the pendant labellum, falls through the flower. This characteristic flight habit of the bee probably has contributed to the evolution of an entirely different system of pollination. Though this kind of flower is distinct, it apparently has been unable to preclude occasional hybrids within the related forms but has simply led to more variation. Color and morphology of the unessential flower parts appear to have been subject to little selection pressure for uniformity, and may vary considerably from plant to plant within a given population. The resulting confusion, caused by attempts to name every variant in cultivation, has not only increased out of all proportion but has tended to make the genus nearly impossible taxonomically.

Stanhopea tricornis occurs frequently in old epiphyte covered cacao trees in the region of Quevedo in central, coastal Ecuador. The species generally succeeds best in fairly dense shade and on a large plant the pendant two-flowered racemes are produced throughout the year. Several racemes may be produced by one pseudobulb.

In late January of 1960 we succeeded in finding a plant which had two open flowers (both had been pollinated) and two mature buds which would open the following day. We removed the plant and carefully carried it to our hotel room. Before dawn of the next morning we found the flowers to be open and emitting a heavy perfume very similar to "Diorissimo" manufactured by the Christian Dior Company of Paris, France. We returned to the cacao plantation at dawn and set the plant in a position where it could be easily photographed. At about 9 a.m. a large male bee, *Eulaema meriana* (Oliv.) (tribe Euglossini, family Apidae, *E. dimidiata* is a synonym) came to the flowers, which he proceeded to investigate, apparently searching for the source of the strong fragrance. Meanwhile a second bee of the same species arrived; neither bee seemed familiar with the flower and each searched for some time before discovering the tunnel-like opening, formed by the petals, column and lip, and entering the flower. It might be noted that this is the only species of *Stanhopea* in which the petals are fleshy and held closely appressed to the column. The bee forced upward past the rostellar spine and entered the inner portion of the flower to the hypochile (see Fig. 4). The bee did not attempt to extract food. In backing out the bee encountered the rostellar spine once again. This time the rostellar spine slid under the posterior projection of the metathorax of the bee, and his struggles dislodged the lance-shaped viscidium of the pollinia, which immediately became cemented to the underside of the metathorax. In further backing out he pulled the pollinia from the anther cap. The bee then flew away. Even if the bee had entered the other flower, pollination could not have been accomplished immediately for the stigmatic pocket of *Stanhopea* does not open sufficiently for insertion of pollinia until several hours after the pollinia have been removed. The following morning what appeared to be a different bee but one with pollinia attached to his metathorax visited the flowers. The pollinia became lodged in the stigma and were removed from the back of the bee, thus effecting pollination. In total, five instances of pollination of *Stanhopea tricornis* were observed with six bees, all *E. meriana*, involved.

Other species of *Eulaema* were noted in the immediate vicinity and were quite curious about the camera, approaching to examine it, but showed no interest in the *Stanhopea tricornis* flowers only a foot or so away. These species were *E. tropica* (Linné) and *E. cingulata* (Fab.)* both of which are responsible for pollinating numerous other orchids including several species of *Catasetum*, *Cycnoches*, *Sobralia violacea* Lindl., *Maxillaria grandiflora* Lindl., *Aspasia epidendroides* Lindl. and *Pescatoria wallisii* Linden & Rchb. f.

From these observations we can glean the following important points:

1. *Eulaema meriana* appears to be the specific pollinator of *S. tricornis*.
2. *Eulaema tropica* and *E. cingulata* are sympatric but showed no interest in *S. tricornis*.
3. *Eulaema meriana* is attracted to the fragrance emitted by *S. tricornis* and without prior experience with the flower must search to find the entrance.

* These identifications have been recently supplied by Dr. Krombein of the Smithsonian Institution. These two species were previously known as *E. musitans* and *E. fasciata* respectively.

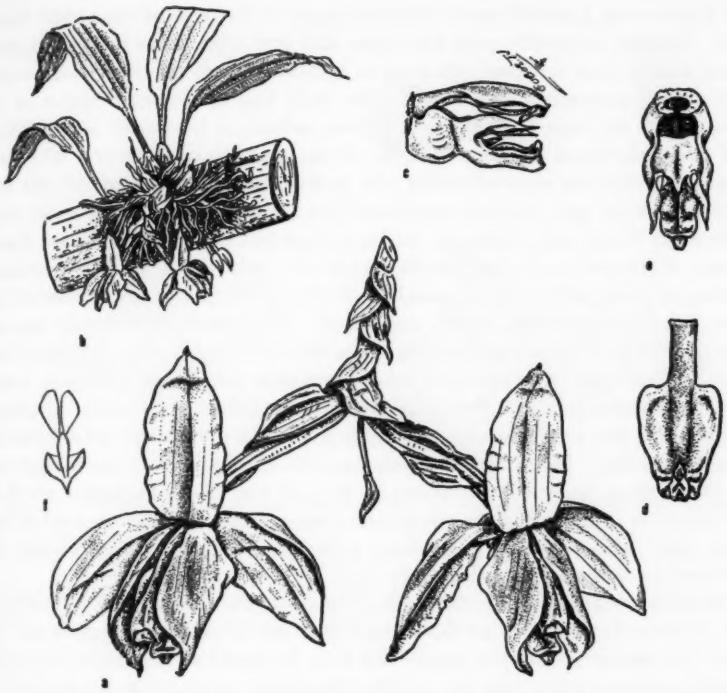


Fig. 9. *Stanhopea tricornis* Lindl. a. Inflorescence (× ⅓). b. Plant habit (× 1/12). c. Side view of the lip (× ⅓). d. Ventral view of the column (× ½). e. Dorsal view of the lip (× ⅓). F. Pollinarium (× 2).

Flower color and structure are certainly secondary if even of importance in the actual attraction of the bee.

Flowers of S. *tricornis* were carefully examined for nectaries or other anatomical structures which would offer food for the bee. None was found. The fragrance is produced in the hypochile; the other parts, when removed from the flower, have little or no fragrance. The inside of the hypochile is covered with long fleshy hairs which the bee might eat but in the flowers entered by *E. meriana* these hairs did not appear to have been disturbed. It appears then, that the bee is attracted strictly on the basis of fragrance and does not receive food. He apparently does not expect to receive food for he does not lower his tongue, which is so long that it must be lowered and swung forward before a narrow flower is entered. This pattern has been observed in other members of the Catasetinae and Stanhopeinae in which male Eulaemas are attracted by the fragrance and the bees do not appear to receive food of any kind.

In all of these orchids the flowers are generally not long lasting but produce their strong, heady, spicy fragrance in such quantity that they can be detected by

the human nose, a notably weak olfactory organ, at distances of more than thirty feet. The bees are usually quite wary when they first come to the flowers but after being around them for some time seem to become drugged for they fly erratically and can be approached easily. Only the male bees of *Eulaema* appear to be attracted to this type of flower; the females, which are busy with nest building and food gathering to provision the nests, do not approach these flowers. The male bees have never been observed taking part in nest building or care of the nest and seem to leave the nest as soon as possible and live a vagabond life. They secure food from many of the same flowers as the female bees but also visit Stanhopeas, Catasetums, Cycnoches and other flowers which offer only the heady and seemingly intoxicating fragrances. It is possible that the female bees are not attracted to these flowers because they cannot sense them. It is known that female bees of *Apis mellifera*, the domestic bee, have fewer olfactory pits in their antennae than do the males. The only orchids in which both male and female bees were noted were *Sobralia violacea* and *Maxillaria grandiflora*. *Sobralia* is a rather primitive orchid which does provide nectar for the bee and which is visited by several bees of different families. *Maxillaria grandiflora* provides starchy hairs at the base of the lip. One morphological feature found in the male bees of the Euglossini which is not present in the females is the presence of chemoreceptive hairs on the tarsi of the front legs. The male bees brush these pads through the scratched surface of the labellum of the orchids which they visit.

Stanhopea bucephalus is pollinated in a somewhat different manner. This variable species is distributed along the western slopes of the Andes from elevations of about 400 meters up to 1200 meters and is to be found on the summits of the coastal mountains where they rise to these elevations. It is sympatric with S. *tricornis* in the region of Quevedo and the two species appear to be sympatric for at least 60 kilometers to the south.

Pollination of this species was observed during the month of March at Olimpo on the railroad from Guayaquil to Quito. Unlike S. *tricornis* this species has thin, narrow petals which became retracted and curl up around the dorsal sepal shortly after the flower opens. The horns are not produced as an extension of the hypochile as in S. *tricornis* but are larger and developed from a definite mesochile. Thus there is left a large open space between the lip and the column at the level of the hypochile. The lower part of the column is effectively surrounded, to form a tunnel, by the horns of the mesochile, the epichile and the wings of the column. The pollinator of this species is also a male *Eulaema*, *E. bomboides* Friese, but this one is only about two thirds as large as *E. meriana*. *Eulaema bomboides* is a little larger than either *E. cingulata* or *E. tropica*.

Eulaema bomboides is attracted by the fragrance of this *Stanhopea* which is honey-sweet, quite unlike S. *tricornis*. The bees come to the flower of S. *bucephalus* but immediately fly into the space between the column and the hypochile and attempt to land on the hypochile, or they land on the side of the hypochile and attempt to crawl around and enter the hypochile to reach the source of the fragrance. The surfaces of all parts of the lip are waxy and extremely slick, so that the bee can not successfully land and hold fast. He falls down and is guided

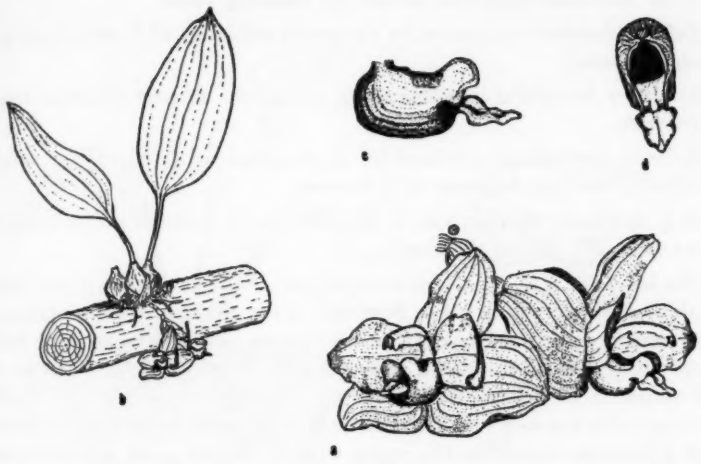


Fig. 10. *Stanhopea reichenbachiana* Roezl. ex Rchb. f. a. Inflorescence (× 1/3). b. Plant habit (× 1/12). c. Side view of lip (× 1/3). d. Dorsal view of the lip (× 1/3).

by the column and its wings at his back, the horns of the mesochile at his sides and the slick epichile beneath him so that he falls directly through the tunnel. At the lower end of the tunnel, almost at its exit, the rostellar spine with the viscidum of the pollinia on its outer surface projects into the path of the falling bee and is caught under the posterior projection of his thorax as in S. *tricornis*. The bee hits the rostellar spine with such force that it gives way and allows the bee to fall through. In doing so the viscidium of the pollinia is cemented firmly into place under the thorax (see Fig. 6). The bee is apparently disturbed and tends to fly away but he repeats the process when he encounters another flower. If the flower is older with an open stigma the pollinia are this time placed in the stigmatic pocket during his fall and pollination is effected.

The pollination of S. *bucephalus* is in many respects quite similar to the pollination of *Gongora maculata* Lindl. as reported by Allen (1956), with the exception that the *Gongora* is pollinated by species of *Euglossa*. *Euglossa* is a genus of bees which is very closely related to *Eulaema* and is also responsible for the pollination of *Coryanthes* (Allen 1950). In *Gongora* the bee, hanging upside down loses its hold on the slick surfaces of the lip, falls and is guided down the pendant column during his fall with the result that he also makes contact with the viscidium of the pollinia much in the same manner as *Eulaema* in S. *bucephalus*.

Several plants of this *Stanhopea* were brought back to the garden of the Instituto Botánico where quantities of *Eulaema tropica* and *E. cingulata* are common and at no time did any of these bees show interest in the flowers. Even when flowering plants of *Catasetum* were placed in the immediate proximity the Eulaemas ignored the *Stanhopea* flowers completely.

From these observations we can add the following facts:

1. *Eulaema bomboides* appears to be the specific pollinator of S. *bucephalus* in the region studied.
2. *Stanhopea bucephalus* is pollinated on an entirely different principle from S. *tricornis*.
3. *Eulaema bomboides* is attracted by the fragrance of S. *bucephalus* which is different from the fragrance of S. *tricornis*.
4. If *E. bomboides* does not visit S. *tricornis* then S. *tricornis* and S. *bucephalus* are effectively isolated genetically.

The last point is by far the most important. *Eulaema meriana* is too large to fall through S. *bucephalus*. If *E. bomboides* is not attracted by the fragrance of S. *tricornis* then the possibilities of the two species of *Stanhopea* forming hybrids are effectively nil. This appeared to be the case. *Stanhopea tricornis* shows very little variability throughout its populations. The sympatric species S. *bucephalus* is quite variable but shows no characters indicating introgression from S. *tricornis*.

If S. *tricornis* evolved in this region with *E. meriana* as its pollinator and S. *bucephalus* was dependent upon a different insect pollinator and a different pollination procedure the two would not hybridize. If by accident a bee of *E. bomboides* did enter S. *tricornis* and effect a hybridization between the two species of *Stanhopea*, and it is feasible that this might occur, then the resulting hybrids would probably find no effective pollinator. If such a pollinator did exist then the chances might be better for development of a completely different, stable species with its own characteristics and its own structurally isolated population.

Interestingly enough, perhaps not all Stanhopeas are pollinated by members of the genus *Eulaema*. The type locality of *Euglossa viridissima* Friese is given as "at *Stanhopea tigrina* at Cordoba and Orizaba in Mexico". If this report is correct, and there is no reason to doubt its validity, it indicates that perhaps some of the species are even more widely separated ecologically than are S. *tricornis* and S. *bucephalus*. Our observations indicate, at least in Ecuador, that Euglossas and Eulaemas are not mutually attracted to the same orchid flowers. Where they are attracted to orchid species of the same genus (i.e., *Eulaema cingulata* is attracted to *Cycnoches lehmanii* and *C. ventricosum* while *Euglossa viridissima* is attracted to *C. egertonianum*) the flowers are extremely distinct morphologically. The principal morphological difference between S. *tigrina* and S. *bucephalus* which would be of importance in pollination procedure lies in the extreme closeness of the column and terminal portions of the lip in the former species whereas in the latter these structures are rather open. A large bee like a *Eulaema* would not be able to fall through S. *tigrina* due to this constriction of parts. On the other hand a *Euglossa* would fall through S. *bucephalus* without touching any of the parts and would be ineffectual in pollination. We feel that the significant factor in this situation does not lie in the morphological form being a deterrent to effective pollination, but rather that the fragrance of the flower does not attract a pollinator which would be ineffective. More likely the morphological structures of the flower have been modified to accommodate the type of pollinator which was attracted to the flower.

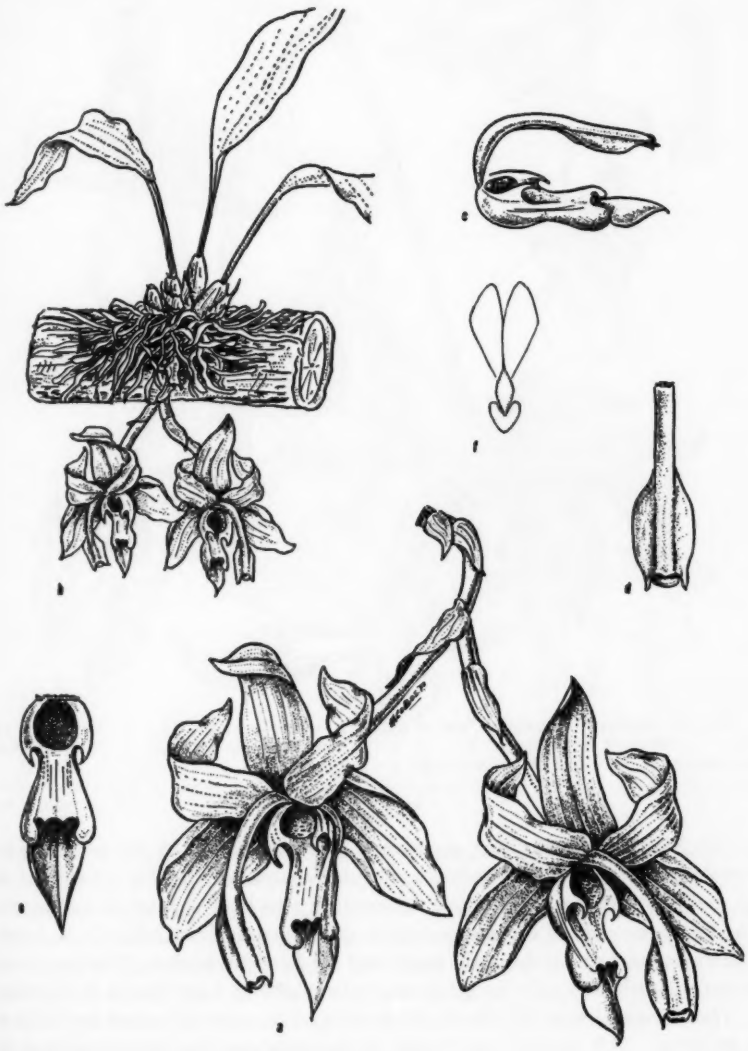


Fig. 11. *Stanhopea grandiflora* (Lodd.) Lindl. a. Inflorescence (× 1/3). b. Plant habit (× 1/8). c. Side view of the lip (× 1/3). d. Dorsal view of the column (× 1/3). e. Dorsal view of the lip (× 1/3). f. Pollinarium (× 3).

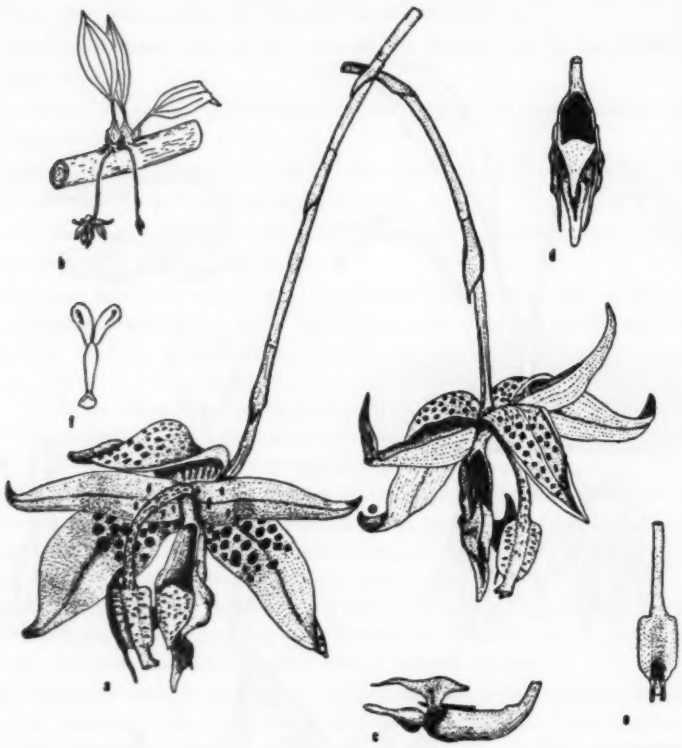


Fig. 12. *Stanhopea rodigasiana* Claes. ex Cogn. a. Inflorescence (× 1/3). b. Plant habit (× 1/15). c. Side view of the lip (× 1/3). d. Dorsal view of the lip (× 1/3). e. Ventral view of the column (× 1/3). f. Pollinarium (× 2).

Variation

We have pointed out that populations of species in *Stanhopea* are often extremely variable. Unfortunately no extensive analysis of specific populations are yet available; however, we did superficially study two large populations in Ecuador. The first occurs along the western slopes of the Andes from Macuchi in northwestern Ecuador to Paccha in the south near the Peruvian border. This population is approximately 400 miles long and ranges from 400 to 1,200 meters in elevation.

Near Macuchi some of the plants correspond to a species named by Rolfe as *S. anfracta.* This species is very close to *S. wardii* and had been considered by Lindley as *S. wardii* var. *venusta.* Schweinfurth (1958) has placed it in synonymy with *S. wardii.* Other plants are similar to what has been known as *S. bucephalus.* The population was sampled at four locations through its central portion and was rather uniformly *S. bucephalus* with only occasional plants occurring which could be considered as referable to *S. wardii.* However, at Santa Isabela near the southern extension of the population the situation changed considerably. Plants were so

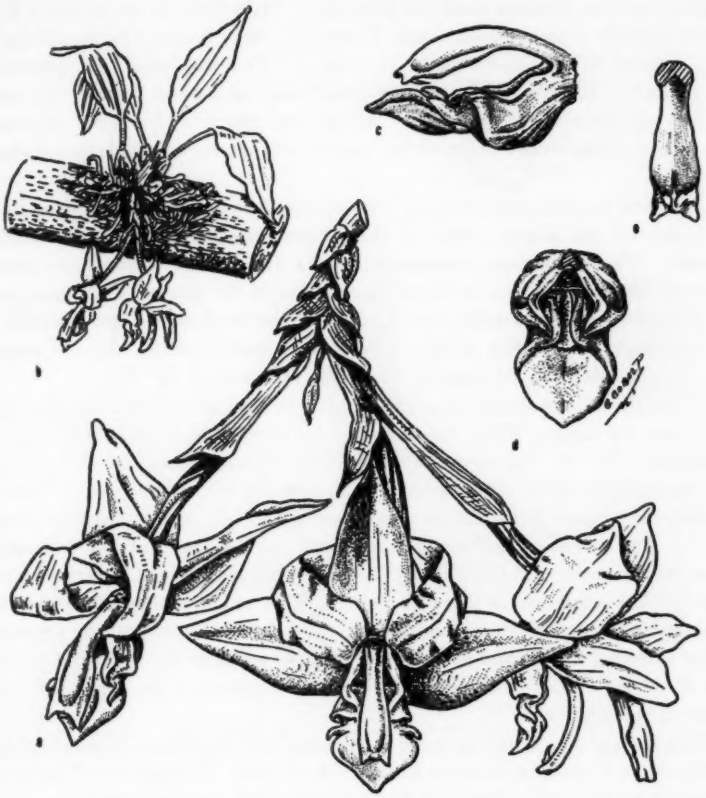


Fig. 13. *Stanhopea lewisae* Ames & Correll. a. Inflorescence (× ½). b. Plant habit (× 1/12). c. Side view of the lip (× ⅔). d. Dorsal view of the lip (× ⅔). e. Ventral view of the column (× ⅔).

variable that specimens were found which corresponded precisely to S. *anfracta*, S. *bucephalus*, S. *graveolens*, S. *oculata*, S. *wardii*, S. *baseloviana*, S. *guttulata*, S. *ornatissima*, S. *platyceras*, and S. *peruviana*. Many plants also occurred in the population which were intermediate between these concepts. Most of these species are actually color forms and many have been relegated to synonymy by other authors. Some of them have been maintained, largely because no botanist knew much about them, for they were described from individual specimens cultivated in Europe and their origins were unknown.

Plants from the population at Paccha, about 20 miles south of Santa Isabela were sent to Europe by a number of early collectors. Kruth named a plant which Humboldt and Bonpland had collected here as *Epidendrum grandiflorum*. Lindley later named another plant from the same locality as S. *bucephalus* and it was illustrated in the Botanical Register, plate 24, in 1845. Reichenbach changed the name to S. *grandiflora*, based on Kunth's name. Another illustration of a plant in the Botanical Magazine, Plate 5278 given as S. *bucephalus* is so inaccurate that four

"species" can be identified from the same plate. Plate 8517 in the Botanical Magazine is actually a plant much nearer S. *wardii*. More recently S. *bucephalus* has been reduced to synonymy under S. *oculata*. This confusion has pointed up the results of describing species from individual specimens without knowledge of the variation within populations. We feel that this situation is not uncommon and clearly demonstrates the need for careful and extensive population studies of the genus.

A second variable population of *Stanhopea* occurs in the valley formed by the headwaters of the Zamora river on the eastern slopes of the Andes in southern Ecuador. The population is extensive and we feel that it demonstrates another of the kinds of phenomena involved in variation of the genus. The upper end of the population reaches a point near Km. 45 on the road from Zamora to Loja, at an elevation of about 1800 meters. The valley is narrow, dense fogs and constant rains are the rule and temperatures are usually low, around 60° F.

Normally the sun breaks through only for an hour or two each day but occasional days are sunny. When the sun is out for several hours the temperature rises to as high as 75° F. The elevation decreases rapidly to the east and at Zamora, 62 km. from Loja, is about 1000 meters. At Zamora the valley levels out and becomes broader, the normal daily temperature is around 75° F. and occasionally reaches 85° F. The weather conditions change little during the year but less rainfall occurs in November and December. The population was studied as far as Yansasa, about 60 km. northeast of Zamora. Here the elevation is near 800 meters and weather conditions are similar to Zamora. In all, the portion of the population studied extended 85 km. and varied from 1 km. in width at the upper end to 3 km. wide at the lower end. Elevations run from 1800 meters at the upper end to 800 meters at the lower end.

Though they are variable in color at the lower end of the population the flowers correspond to *Stanhopea anfracta* Rolfe. The flowers of plants at the upper end are similar to the species described by Schlechter as S. *peruviana* and demonstrate little variation. Both of these species have been reduced to synonymy under S. *wardii*. A cline occurs from the upper end of the population to the lower, the plants in the center having flowers essentially intermediate between the extremes. Variation increases considerably toward the lower end of the population. Vegetatively the plants are indistinguishable throughout the population.

The flowers of the plants at the upper end of the population are morphologically nearly identical to the flowers at the opposite extremes but are colored quite differently and are much thicker in substance. The flowers are completely tangerine-yellow with no other color involved. The sepals and petals have heavy texture and are not reflexed. The flowers usually last for eight days.

At the lower end of the population the flowers are thin in substance and have their sepals and petals strongly reflexed. The basal part of the lip, sepals and petals are yellow-orange flecked and spotted with maroon-red, and the extremities of the sepals, petals and lip are white flecked with red. The flowers last only one or two days. Plants from around Zamora had flowers more or less intermediate between the two extremes in all characters.

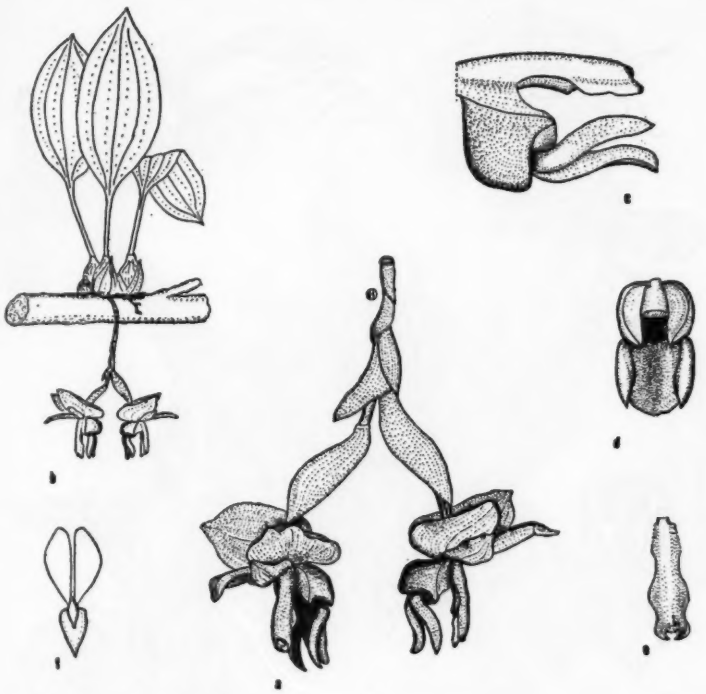


Fig. 14. *Stanhopea connata* Rchb. f. a. Inflorescence (× ⅕). b. Plant habit (× 1/6). c. Side view of the lip (× ⅔). d. Dorsal view of the lip (× ½). e. Dorsal view of the column (× ½). F. Pollinarium (× 2).

From Zamora to Yansasa bees of the genus *Eulaema* were very common. One species in particular was quite common and appeared much like *E. bomboides*. They were of the same size but slightly different in color pattern and probably represent *E. nivofasciata* Friese. Though none was actually observed pollinating Stanhopeas it is probable that they are the pollinators. *Eulaema cingulata* was also common and while they visited other flowers placed in proximity they showed no interest in Stanhopeas and would not enter them.

The bees of this genus are partial to the warmer tropical climates. They nest in hollow limbs or in holes in embankments and their nests have not been encountered at elevations above 1,000 meters in Ecuador. From Zamora to Yansasa they are commonly observed visiting *Costus, Inga* and *Bixa*. They are fast flying bees and are capable of long flights. They are seldom seen in the upper end of the valley and then only on the rare, sunny, warm days. It would appear that they do not nest in the upper extensions of the valley. Plants in the lower regions commonly produce one or two seed capsules indicating considerable visitation by the insects. In the upper regions, on the other hand, seed capsules are rarely encountered.

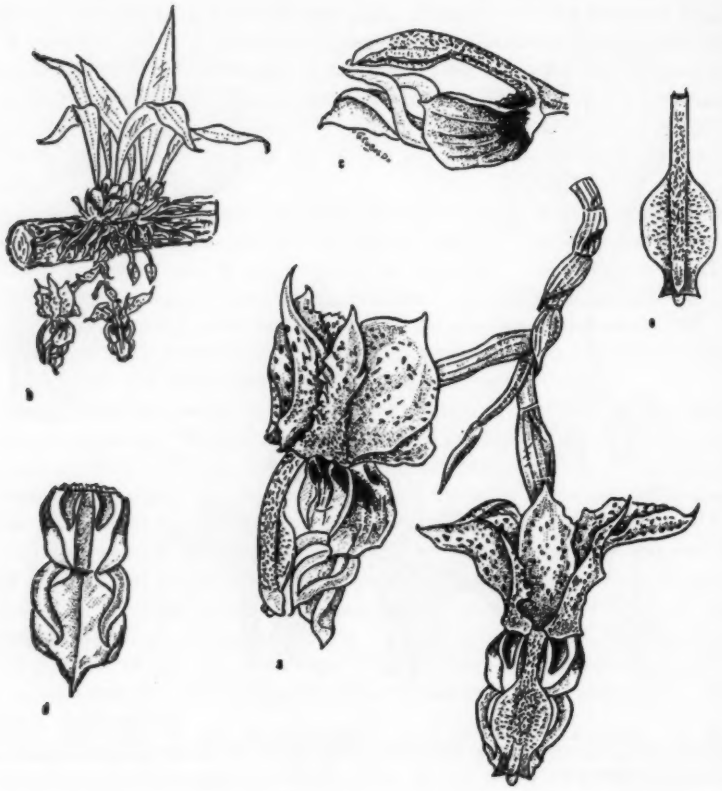


Fig. 13. *Stanhopea insignis* Frost. a. Inflorescence (× ⅓). b. Plant habit (× 1/12). c. Side view of the lip (× ½). d. Dorsal view of the lip (× ½). e. Dorsal view of the column (× ½).

This population in some respects appears rather typical of the populations of *Stanhopea* in Ecuador. It is not as complex as the population of *Stanhopea* on the western slope of the Andes which is extremely variable in the direction of S. *wardii* in its northern portion, rather stable in its central portion corresponding to S. *bucephalus* and mixed with typical S. *oculata* in its southern extension. It is our opinion that this type of variation is typical of S. *oculata* and allied species throughout their range. It would appear that the relatively stable, heavy substanced, long lasting type of flower at the upper extension of the Zamora population may be due to strong natural selection for that type of flower. In the upper elevations where pollinators are not abundant it would be of more value to the population to have long lived flowers which would have a greater possibility of visitation and pollination. Such flowers may have to wait several days for weather conditions to be satisfactory for bees to reach them. Short lived flowers would stand little chance of being visited and therefore would rarely reproduce. Long life in these flowers depends on thickness of their parts. A selection pressure is therefore exerted for



Fig. 16. *Stanhopea tigrina* Batem. a. Inflorescence (× ⅓). b. Plant habit (× 1/6). c. Side view of the lip (× ½). d. Dorsal view of the lip (× ⅓). e. Dorsal view of the column (× ½).

flowers with heavy substance. In the lower regions flowers are normally visited shortly after opening and long lived flowers would offer no selective advantage.

Some botanists would attempt to attribute such extreme population variability as is found in *Stanhopea* to hybridization and introgression. Perhaps this is a partial answer but in many cases the variable populations are so widespread as to preclude hybridization. One might also suggest that the variation is due to high mutation rate. Perhaps this is also a partial answer. It is apparent from what has been pointed out above in the pollination section of this paper that the bees which accomplish the pollination are attracted by the strong fragrance of the flowers. The color, and to a degree, the form of the flower appears to be of minor importance in its pollination. This is also true in the genera related to *Stanhopea*, such as *Gongora* and *Coryanthes*.

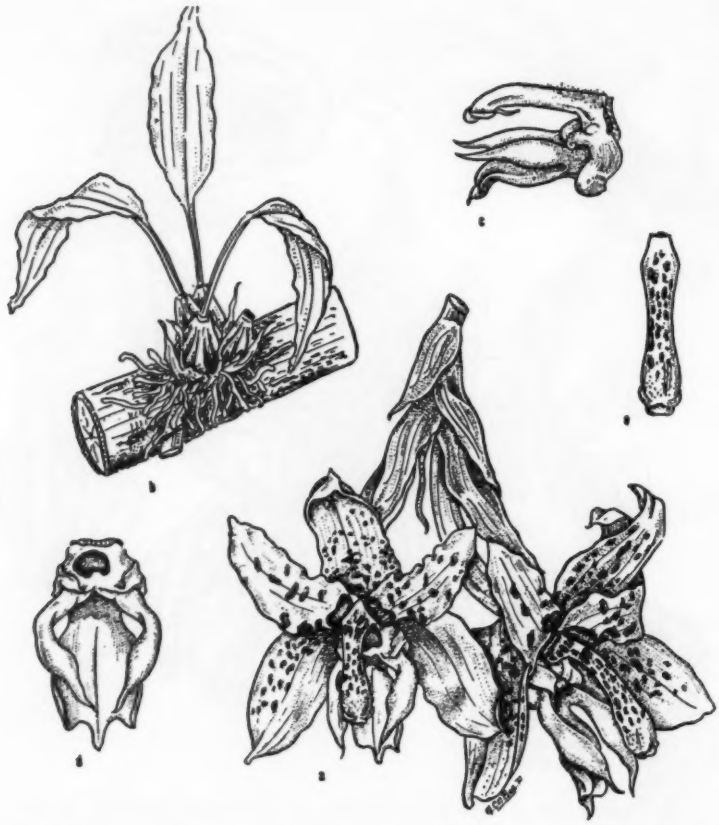


Fig. 17. *Stanhopea martiana* Batem. ex Lindl. a. Inflorescence (× ⅓). b. Plant habit (× ⅒). c. Side view of the lip (× ½). d. Dorsal view of the lip (× ½). e. Dorsal view of the column (× ½).

If the attraction of the fragrance is so strong, color may be a minor factor in selection and the bees will still visit the flowers even if color varies widely. Also form could vary widely in parts which are not essential to the actual mechanisms of pollination, allowing variants due to mutation to remain within the population as fully effective breeding members contributing to the gene pool as a whole. In S. *oculata* and its allied species the characters which vary the most are the form of the hypochile of the lip and the color of the lip, sepals and petals. These are characters which are not actually involved in the mechanisms of pollination, and may not be important in the actual attraction of the pollinator. Selection would not be strong for these characters and a plant which deviated from the norm to a considerable extent could still remain a breeding member of the population as long as it retained the character of fragrance to attract the pollinator and the correct propor-



Fig. 18. *Stanhopea saccata* Batem. a. Inflorescence (× ⅓). b. Plant habit (× 1/15). c. Side view of the lip (× ½). d. Dorsal view of the lip (× ½). e. Dorsal view of the column (× ½).

tions of the tunnel of the lip, formed by the mesochile and column, to properly place the pollinia for transport by the bee to another flower.

The fact that cross-pollination is nearly obligate in these genera may be of importance also. Certainly more variation would be produced, maintained and dispersed in a population of obligate cross-pollinating plants than in a population where self-pollination is possible and often of regular occurrence. Certain of the genera in the Catasetinae, i.e., *Catasetum* and *Cycnoches*, are characterized by unisexual flowers which make cross-pollination obligate. These are genera in which the species are notoriously variable. In many of the other genera self-

incompatibility is the rule. Not a great deal of information is available on this phenomenon but the authors have made numerous attempts to self-pollinate *Stanhopea bucephalus* and *Gongora maculata* with no success. The resulting seed pods dropped after a few weeks.

In most of these variable genera the flowers are highly fragrant but extremely short lived, seldom lasting more than two or three days. The fragrance ceases very soon after the flower has been pollinated. It would appear that there is a correlation involved between the characteristics of powerful fragrance and short lived flowers. These species seem to depend on their fragrance to attract pollinators and are usually very successful, for a considerable portion of the flowers are pollinated. They have developed in the direction of stronger and more attractive fragrances but offer no food or nectar to the pollinator. Selection may even favor short-lived flowers which do not attract bees long after their pollination (i.e., do not compete with the younger flowers). Here there seems to be a strong selection pressure for fragrance for pollinator attraction with lower selection pressure for constancy of morphological characters.

Many of the orchids which have long lasting flowers are either not fragrant or are weakly fragrant. These orchids seem to depend on numbers of flowers few of which are ever pollinated. These species for the most part are not as variable as the fragrant types and have developed other mechanisms for attraction of the pollinator. Where populations of these species are extremely variable, it is usually in a relatively limited geographical area and their variability can often be attributed to introgressive hybridization.

SUCCESSFULNESS OF THE GENUS

The objective measurement of success in a group of plants is difficult, as too many factors are involved. Obviously, so called weedy species would rate high on the scale. However, to attempt to rate other plants as being highly successful or only fairly successful is scarcely possible. We do feel, however, that we can subjectively rate the success of a group of orchids in relation to other orchids. In such a subjective sense we can use extent of distribution and density of populations as measuring tools. Many orchids are highly successful in respect to density of population but are limited in distribution. Others have wide distributions but are seldom encountered in quantity in a given area. The majority of the species of *Stanhopea* are in one or the other of these categories. The "*insignis* and *oculata* complexes" on this basis are highly successful in that they are commonly found in quantity (in undisturbed habitats) and have broad ranges. They are to be encountered in any region of the American tropics which provides the basic needs of the plants. They are found from sea level to 7000 feet and grow as well in either location provided there exists sufficient humidity and shade and the temperatures are not too low.

This very success, we feel, contributes to their variability, but on the other hand, may have suppressed speciation. The extremes of the range may be expected to produce forms which are unlike due simply to spatial relations. However isolation is difficult to achieve in a dense and essentially continuous population. In

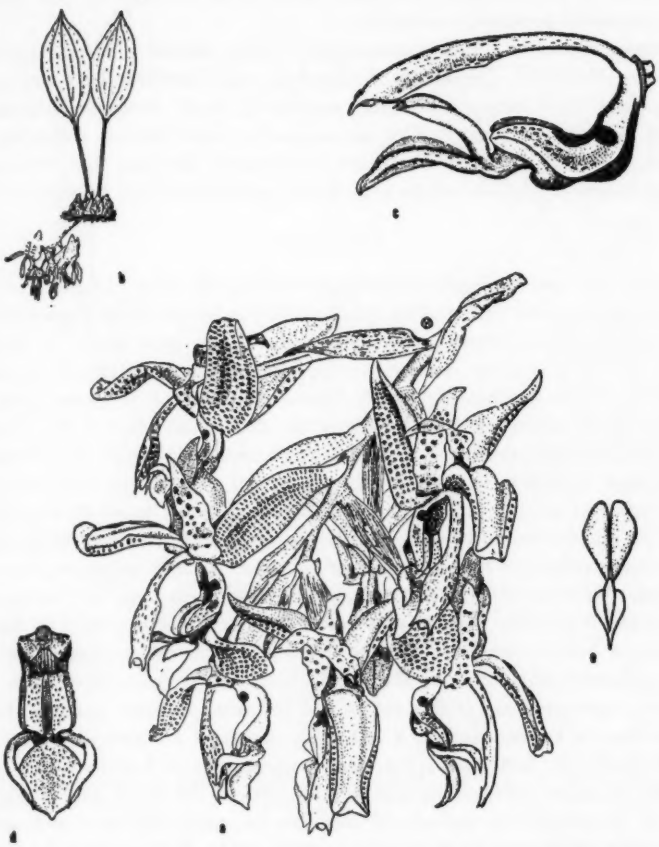


Fig. 19. *Stanhopea oculata* (Lodd.) Lindl. a. Inflorescence (× ⅓). b. Plant habit (× 1/15). c. Side view of the lip (× ⅔). d. Dorsal view of the lip (× ½). e. Pollinarium (× 2).

this respect "success" and taxonomic diversity may be mutually incompatible.

This situation is by no means limited to *Stanhopea*. The hooded types of *Catasetum* reflect the same phenomena, though not quite to the same degree. In Mexico and middle Central America a form known as *C. integerrimum* Hook. is common and variable. Further south in Costa Rica and Panama intergrading populations known as *C. viridiflavum* Hook., *C. oerstedii* Rchb. f. and *C. maculatum* Kunth occur. From Panama extending through Venezuela, the Guianas and northern Brazil the form known as *C. macrocarpum* L. C. Rich. is found. In Ecuador *C. macroglossum* Rchb. f. is common. All of these populations are highly variable and in Ecuador alone, specimens corresponding to all of these "species" may be found. There is little reason to recognize these species when they are now known to be only representatives of one widely distributed and highly successful popula-

tion. Here, as in *Stanhopea*, speciation seems to be inhibited by the otherwise highly successful population structure.

Gongora maculata Lindl. demonstrates a close parallel. Several species of *Cycnoches, Mormodes, Coryanthes, Epidendrum* and *Oncidium* have similar patterns. Many other instances of highly successful, widely distributed orchids can be given in which the most striking chracteristic is their extreme variability. We feel that speciation has taken a back seat to success in the sense that development of distinct taxa is inhibited where gene flow is unrestricted and selection is weak.

TAXONOMY

Perhaps the most successful method of handling the great variability in *Stanhopea* will be to follow that used by Allen (1952) in his particularly workable and useful revision of *Cycnoches*. *Cycnoches* reflects the same kinds of problems encountered in *Stanhopea* and by placing several closely related, intergrading populations, which had been previously known as species, as subspecies under one inclusive species, Allen was able to indicate the close relationships of these populations. In our opinion this is the most practicable manner to handle the problems of such extreme variability in obviously closely related populations. Certainly, it is folly to attempt to apply species or even subspecies names to all of the variants found; the number would be endless. There may be some difference of opinion as to how many subspecies should be recognized, some authors suggesting more and others less. When numerous well authenticated population studies are accomplished in *Stanhopea* it is quite possible that certain of the dubious species within the "*insignis* and *oculata* complexes" will be found to exist as discrete populations and will be sufficiently distinct to be recognized, others will probably be reduced.

Recent correspondence with a rather well informed amateur orchid enthusiast indicates that he has encountered a stable population of a *Stanhopea*. Specimens which he has kindly forwarded appear near the type form of S. *oculata*. He maintains that these are different from typical S. *oculata*, are stable within what he knows of the population and should therefore be recognized as a new species. Perhaps with exhaustive study this population might be found to be distinct throughout its extent and should therefore be considered as a valid species. Our experience with populations of *Stanhopea* in Mexico, Guatemala, Costa Rica, Panama, Ecuador and Peru would indicate that this population, throughout its entire range, would very doubtfully represent even a valid subspecies of S. *oculata*. This case, however, is quite representative of the problems which *Stanhopea* offers and indicates the necessity of thorough knowledge of large percentages of over-all populations before rash action is taken in applying more epithets in the group.

The nomenclature of *Stanhopea* is badly confused and the efforts made by modern workers to clarify the situation have not always been particularly successful. Many of the early descriptions of the species were not accompanied by illustrations and were at best brief. Several of them are nearly impossible to identify with any particular population. One of the unfortunate pitfalls the modern taxonomist encounters is the tendency to make one of these early descriptions fit his concept of a given species or vice versa. Normally the taxonomist has the type specimen

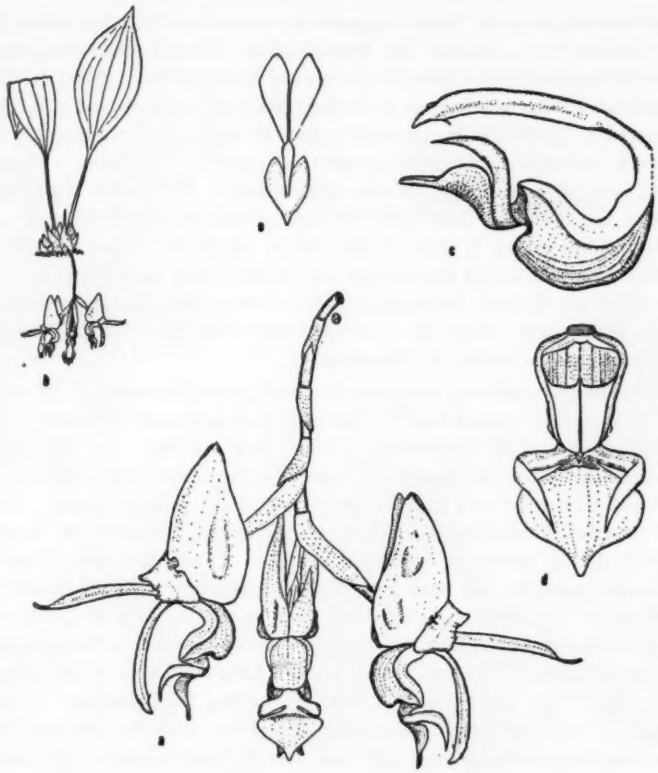


Fig. 20. *Stanhopea bucephalus* Lindl. a. Inflorescence (× 1/3). b. Plant habit (× 1/15). c. Side view of the lip (× 2/3). d. Dorsal view of the lip (× 2/3). e. Pollinarium (× 2).

to fall back on and this specimen, when carefully examined, supplies the necessary information to avoid error. Unfortunately, herbarium specimens of Stanhopeas do not always fulfill this function even when they exist. The critical characters which separate species in this genus are for the most part destroyed in the preparation of specimens.

Many times the type specimen does not reflect the actual structure of the population. An example is to be found in *S. wardii* in which the type description mentions two teeth produced at the base of the hypochile by the extension of the falcate lateral margins. This character is common in the specimens from southern Central America and perhaps to a lesser extent in Guatemala, but actually does not occur in many of the specimens from Mexico, Nicaragua and northern South America, which are certainly referable to this species on every other criterion. To further complicate the situation, this character does occur occasionally in other species such as *S. oculata* and *S. bucephalus*. Doubtless, the type specimen of *S. wardii* did have this character, but the presence or absence of this one character,

since it is not diagnostic of the total population and is found in other species, should not be considered as a criterion for determination. Several other characters help to make this species distinct from S. *oculata* and S. *bucephalus*. Allen (1949) has suggested that Lindley was in error in his description of S. *oculata* and S. *bucephalus*. Allen placed S. *bucephalus* in synonymy under S. *oculata* and re-erected S. *graveolens* which had been considered as synonymous with S. *bucephalus*. We cannot, however, agree with Allen and feel that the epithet, S. *bucephalus*, should be used in place of S. *graveolens*. Since Lindley's descriptions are extremely brief and the later illustrations which he used of his species correspond rather well with his descriptions and with actual populations, we feel that Allen has allowed his splendid knowledge of the Central American species to overshadow the variation of these species in other areas. Since the type specimens yield little information it will always be difficult to resolve this situation.

Another of the confusing situations involved in the taxonomy of *Stanhopea* is the use of the name "*grandiflora*". This name was first used by Kunth when he described and illustrated *Epidendrum grandiflorum* in 1808. In 1828 Loddiges described another plant and named it *Ceratochilus grandiflorus* but the name *Ceratochilus* had previously been used by Blume for an East Indian orchid. In 1832 Lindley transferred the Loddiges plant to the genus *Stanhopea* of Frost and described a similar species as *Stanhopea eburnea*. Later these two plants were found to be conspecific but have been known as S. *eburnea* to the present time. Lindley's name, S. *grandiflora*, is valid and must be used in place of S. *eburnea*. In 1832 Lindley also named a plant which was essentially identical to Kunth's plant as *Stanhopea bucephalus*. The type specimen was a Ruíz and Pavón collection which, as Rolfe (1912) has pointed out, is marked as being from Mexico. It appears that many of Ruíz and Pavón's specimens were mixed with the Sessé and Mociño Mexican collections and a great deal of confusion has been caused by this situation. The probable origin of the Ruíz and Pavón specimen was Peru, as it was then called, or what is now Ecuador. It must have come from very near the same locality as Kunth's specimen since the trails of access to the Andes were very few during this period.

Reichenbach apparently attempted to clear up the situation by transferring Kunth's plant to *Stanhopea* and reducing Lindley's S. *bucephalus* to synonymy under S. *grandiflora* Rchb. f. Unfortunately, Reichenbach's S. *grandiflora* is invalid because Lindley's combination precedes it.

Another attempt to clarify the situation in the "*insignis* complex" has been the reduction of the name S. *tigrina* Batem. to synonymy under S. *devoniensis* Lindl. by Williams (1951). However, the concept, early descriptions, and illustrations of S. *devoniensis* and S. *tigrina* appear to us to be clearly distinct. The plate of S. *devoniensis* in Lindley's *Sertum Orchidacearum* has little resemblance to Bateman's plate of S. *tigrina* in his *Orchids of Mexico and Guatemala* and very likely represents either a rarely encountered species or a hybrid form between S. *saccata* and S. *tigrina*. The figure very definitely resembles S. *saccata* in the features of the lip more closely than it does S. *tigrina*. Williams may have been misled by the color, and was certainly handicapped by the lack of good type material. Occasionally

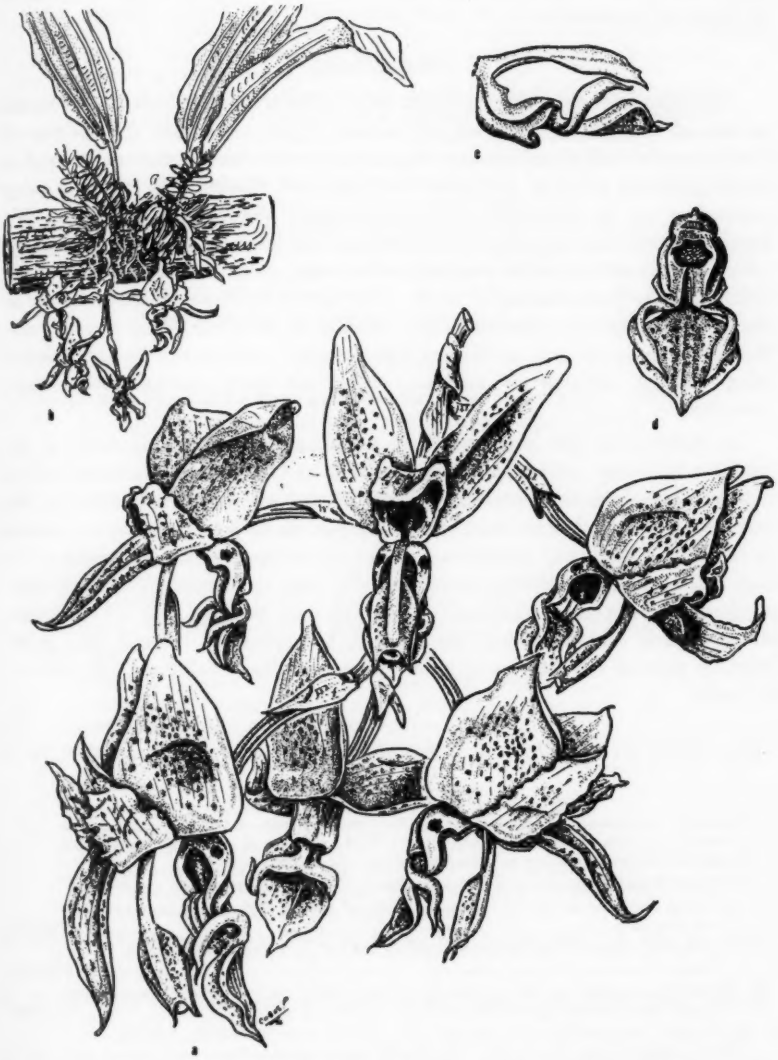


Fig. 21. *Stanhopea wardii* Lindl. a. Inflorescence (× ⅓). b. Plant habit (× 1/6). c. Side view of the lip (× ½). d. Dorsal view of the lip (× ½).

plants with flowers somewhat like the description and plate (discounting the three-lobed epichile which is lacking in the plate but mentioned in the description) turn up, but are quite rare in comparison to the number of typical S. *tigrina* found in the Mexican populations.

CONCLUSIONS

This paper has been written as a discussion of *Stanhopea* preliminary to a formal revision of the genus. Our original intention was to include the revision of *Stanhopea* with this paper but after examination of herbarium material proved to be disappointing we have concluded that only with further field study of living populations can we accomplish a truly meaningful treatment of the genus. We have also found that to merely revise *Stanhopea* and leave the other members of the subtribe Stanhopeinae in the condition which they are at the present time would be to do a less than meaningful work. The members of the Stanhopeinae are so closely intermeshed with *Stanhopea* that revision of the whole group is mandatory. We hope that in the not too distant future such a revision can be accomplished using classical methods of taxonomy combined with modern biosystematic procedures.

In reality then, this paper can only point up the problems involved in the group; it brings up to date the information that is available from the literature and adds our own limited observations of the natural phenomena occurring in the group. These field observations have pointed out the path, so to speak, that should be followed in the study of such a complex and difficult genus as *Stanhopea*. It may well be true that similar procedures will need to be used in treating other problem groups in the Orchidaceae. Our experience indicates that future studies of the difficult subtribe Catasetinae can only be approached through field study. Probably parts of the Sobraliinae, Epidendrinae and Pleurothallidinae will prove to be similar.

APPENDIX

KEY TO STANHOPEA

a. Lip simple, composed of a saccate hypochile with thickened midlobe forming a non-articulated epichile, mesochile absent; column thick, wingless or narrowly winged with the apex of the wings caudate and extended beyond the anther.

b. Hypochile entire, not projected into side lobes on its upper edges; column wingless.

c. Callus in center of the lip tongue-like, apex of the lip slightly thickened; lip 3.8–4.5 cm. long.....1. S. ECORNUTA

cc. Callus in center of the lip absent, apex of the lip thick and fleshy; lip 1.8–2.5 cm. long.....2. S. PULLA

bb. Hypochile projected into fleshy lobes on its upper edges; column narrowly winged with the apex of the wings caudate and extended beyond the anther.....3. S. CIRRHATA

aa. Lip complex, composed of 2 or 3 distinct parts, epichile articulated to the hypochile or to a fleshy mesochile that is provided with lateral horns; column slender and arcuate with narrow or broad wings which are not caudate at their apex and extended beyond the anther.

b. Petals erect and fleshy, paralleling the lip and column; mesochile of the lip consisting of 3 horns, one large lanceolate horn on each side and a third horn produced from the center of a fleshy plate between and extending over the epichile.....4. S. TRICORNIS

bb. Petals thin in substance and reflexed; mesochile of the lip with 2 horns on its margins or none.

c. Hypochile of the lip provided with 2 distinct horns or protuberences, mesochile relatively simple and without lateral horns.
d. Hypochile subsaccate provided with fleshy lobes on each side of the apex; column narrowly winged.....5. S. REICHENBACHIANA
dd. Hypochile relatively slender, horns at base slender and recurved, lobes at the apex not fleshy; column broadly winged.....6. S. GRANDIFLORA
cc. Hypochile of the lip with the lateral margins thickened, not provided with horns or protuberences, mesochile with 2 distinct horns.
d. Horns of the mesochile divided at their midpoint to produce a falcate, retrorse appendage as well as a slender forward projecting spine; flowers always solitary.....7. S. RODIGASIANA
dd. Horns of the mesochile acicular or flat, not divided; flowers normally 2 or more.
e. Horns of the mesochile very short, free for less than 1 centimeter.....8. S. LEWISAE
ee. Horns of the mesochile long, free for more than 2 centimeters.
f. Mesochile obsolete, very short, hypochile conspicuously adnate to the column.....9. S. CONNATA
ff. Mesochile conspicuous, well developed, hypochile not adnate to the column.
g. Hypochile globose or saccate.....10. *insignis* complex
gg. Hypochile more or less elongate or quadrate.....11. *oculata* complex

List of Species*

1. STANHOPEA ECORNUTA Lem. in Fl. des Serres 2: *t. 181.* 1846. (Fig. 6).
Stanhopea calceolus Hort. ex Rchb. f. Xen. Orch. 1:117. 1858.
Stanhopeastrum ecornutum Rchb. f. Xen. Orch. 1:124. 1858.
2. STANHOPEA PULLA Rchb. f. in Gard. Chron. 7:810. 1877. (Fig. 7).
3. STANHOPEA CIRRHATA Lindl. in Journ. Hort. Soc. 5:37. 1850. (Fig. 8).
4. STANHOPEA TRICORNIS Lindl. in Journ. Hort. Soc. 4:236. 1849. (Fig. 9).
†*Stanhopea stenochila* Lehm. & Kranzl. in Gard. Chron. 369. 1900.
†*Stanhopea langlasseana* Cogn. in Gard. Chron. 426. 1901.
Stanhopea convulata Rolfe, in Kew Bull. 366. 1909.
5. STANHOPEA REICHENBACHIANA Roezl. ex Rchb. f. in Gard. Chron. 2:40. 1879. (Fig. 10).
Stanhopea amesiana Hort. ex Gard. Chron. 352. 1893.
†*Stanhopea lowii* Rolfe, in Kew Bull. 63. 1893.
Stanhopea suavis Hort. in Ospina, Orquidas Colomb.
6. STANHOPEA GRANDIFLORA (Lodd.) Lindl. Gen. & Sp. Orch. 158. 1832. (Fig. 11).
Ceratochilus grandiflorus Lodd. in Bot. Cab. *t. 1414.* 1828.
Stanhopea eburnea Lindl. in Bot. Reg. 18: *t. 1529.* 1832.
Stanhopea calceolata Hort. ex Rchb. f. 1:117. 1858.
Stanhopea calceolata Drap. Lenq. Hort. Univ. 2:127 & 264.
†*Stanhopea candida* Barb. Rodr. Gen. Spec. Orch. Nov. 1:101. 1877.
Stanhopea randii Rolfe, in Kew Bull. 363. 1894.
7. STANHOPEA RODIGASIANA Claes. ex Cogn. in Gard. Chron. 14. *Fig. 9.* 1898. (Fig. 12).
8. STANHOPEA LEWISAE Ames & Correll, in Bot. Mus. Leafl. Harv. Univ. 10^4:86. Pl. 10. 1942. (Fig. 13).
9. STANHOPEA CONNATA Kl. in Otto & Deitz. Alleg. Gartenz. 22:226. 1854. (Fig. 14).
Stanhopea graveolens Kl. ex Rchb. f. Xen. Orch. 1:118. 1879

* The names placed in synonymy in this list have been previously reduced by other authors with the exception of those marked thusly: †.

10. "*insignis* complex"

STANHOPEA INSIGNIS Frost ex Hook. in Bot. Mag. *t. 1948 & 1949.* 1829. (Fig. 15).

Stanhopea flava Lodd. ex Beer. Prakt. Stud. Fam. Orch. 312. 1854.
Stanhopea atropurpurea Lodd. ex Planch. Hort. Donat. Orch. 215. 1858.
Stanhopea odoratissima Hort. ex Planch. Hort. Donat. Orch. 216. 1858.
Stanhopea macrochila Lem. in Illustr. Hort. 4: Misc. 71. 1859.

STANHOPEA TIGRINA Batem. ex Lindl. Sert. Orch. 1. 1838. (Fig. 16).

Stanhopea cavendishii Lindl. ex Batem. Lond. Hort. Brit. Suppl. 3:643.
Stanhopea maculosa Knowles & Westc. Flor. Cab. 3: *t. 121.* 1839.
Stanhopea nigroviolacea Morren. ex Beer. Prakt. Orch. 313. 1854.
Stanhopea expansa P. N. Don. Hort. Cantab. 13:721. 1845.
Stanhopea lyncea P. N. Don. Hort. Cantab. 13:608. 1845.

STANHOPEA DEVONIENSIS Lindl. Sert. Orch. *t. 1.* 1838.

STANHOPEA MARTIANA Batem. ex Lindl. in Bot. Reg. 26: Misc. 50. 1840. (Fig. 17).

Stanhopea velata Morren, in Ann. Soc. Gand. 3. *t. 153.* 1847.

STANHOPEA SACCATA Batem. Orch. Mex. & Guatem. *t. 15.* 1839.

Stanhopea implicata Westc. ex Lindl. Fol. Orch. Stan. 6. 1852.
Stanhopea radiosa Lem. Illustr. Hort. 4: Misc. 72. 1859.
Stanhopea marshii Rchb. f. Xen. Orch. 1:120. 1879.
Stanhopea elegantula Rolfe, in Kew Bull. 161. 1910.

STANHOPEA INTERMEDIA Kl. in Act. Hort. Petrop. 17:142. 1898.

11. "*oculata* complex"

STANHOPEA OCULATA (Lodd.) Lindl. Gen. & Sp. Orch. Pl. 158. 1832. (Fig. 19).

Ceratochilus oculatus Lodd. in Bot. Cab. *t. 1764.* 1832.
Stanhopea lindleyi Zuccar, Abh. Akad. Muenich 2:320. 1831–33.
Stanhopea guttulata Lindl. in Bot. Reg. 29: Misc. 75. 1843.
Stanhopea graveolens Morren in Ann. de Gard. 2:55. *t. 54.* 1846.
Stanhopea guttata Kich. Berl. Allg. Gartenz. 364. 1858.
Stanhopea ornatissima Lem. in Illustr. Hort. 9:325. 1862.
Stanhopea cymbiformis Rchb. f. Xen. Orch. 2:84. *t. 124.* 1865.
Stanhopea minor Schltr. Notizbl. Bot. Gart. Mus. Berlin 6:483. 1917.

STANHOPEA BUCEPHALUS Lindl. Gen. & Sp. Orch. Pl. 157. 1832. (Fig. 20).

Stanhopea graveolens Lindl. in Bot. Reg. 3: Misc. 59. 1840.
Stanhopea aurantia Lodd. ex P. N. Don in Hort. Cantab. 608. 1845.
Stanhopea jenishiana Kramer ex Rchb. f. Bot. Zeit. 10:934. 1852.
Stanhopea warscewicziana Kl. in Allg. Gartenz. 20:214. 1852.
Stanhopea guttata Beer. Prakt. Orch. 312. 1854.
Stanhopea inodora Rchb. f. Xen. Orch. 2:157. 1858.
Stanhopea aurata Hort. ex Planch. Hort. Donat. Orch. 104. 1858.
Stanhopea aurata Beer, Prakt. Stud. Fam. Orch. 310. 1858.
Stanhopea costaricensis Rchb. f. in Hamb. Gartenz. 16:424. 1860.
Stanhopea grandiflora Rchb. f. Walp. Ann. 6:587. 1863.
Stanhopea oculata var. *constricta* Kl. in Acta Hort. Petrop. 17:15. 1898.
Stanhopea lietzei Schltr. in Fedde Rep. Sp. Nov. 16:248. 1919.
Stanhopea remota Hort.

STANHOPEA WARDII Lodd. ex Lindl. Sert. Orch. *t. 20.* 1838. (Fig. 21).

Stanhopea aurea Lodd. ex Lindl. in Bot. Reg. 4: Misc. 11. 1841.
Stanhopea venusta Lindl. in Bot. Reg. 4: Misc. 11. 1841.
Stanhopea inodora Lodd. ex Lindl. in Bot. Reg. *t. 65.* 1845.
Stanhopea amoena Kl. in Allg. Gartenz. 20:273. 1852.
Stanhopea anfracta Rolfe, in Orch. Rev. 12:357. 1904.
Stanhopea purpusii Schltr. in Orchis 10:186. 1916.
Stanhopea peruviana Rolfe, in Bot. Mag. *t. 8417.* 1912.

Species too poorly known to place at present

Stanhopea annulata Mansf. in Orchis 16:19. 1938.
Stanhopea bicolor C. Koch. Berl. Allg. Gartenz. 209. 1857.
Stanhopea deltoidea Lem. in Illustr. Hort. 9:340. 1862.
Stanhopea florida Rchb. f. in Gard. Chron. 615. 1879.
Stanhopea fregeana Rchb. f. in Otto & Dietr. Allg. Gartenz. 23:313. 1855.
Stanhopea fuerstenbergiae Kranzl. in Gard. Chron. 161. 1899.
Stanhopea gibbosa Rchb. f. in Gard. Chron. 1254. 1869.
Stanhopea haseloviana Rchb. f. in Otto & Dietr. Alg. Gartenz. 23:322. 1855.
Stanhopea hoppii Schltr. in Fedde Rep. Sp. Nov. 27:82. 1924.
Stanhopea impressa Rolfe, in Kew Bull. 196. 1898.
Stanhopea madouxiana Cogn. in Gard. Chron. 134. 1898.
Stanhopea moliana Rolfe, in Lindenia 7:89. *t. 331*. 1891.
Stanhopea nigripes Rolfe, in Kew Bull. 364. 1894.
Stanhopea platyceras Rchb. f. in Gard. Chron. 27. 1868.
Stanhopea ruckeri Lindl. in Bot. Reg. subt. 44. 1843.
Stanhopea schilleriana Rchb. f. Xen. Orch. 2:158. 1858.
Stanhopea shuttleworthii Rchb. f. in Gard. Chron. 795. 1876.
Stanhopea uncinata Drap. Hort. Univ. 4:65. 1843.
Stanhopea xytriophora Rchb. f. in Gard. Chron. 842. 1868.

Dubious species

Stanhopea quadricornis Lindl. in Bot. Reg. 24: *t. 5*. 1838.

Obscure species

Stanhopea russelliana Lodd. ex P. N. Don in Donn. Hort. Cantab. 13:721. 1845.
Stanhopea violacea Hort. ex Beer. Beitr. Morph. u Biol. Orch. *t. 4 & 8*. 1863.
Stanhopea wallisii Rchb. f. in Linnaea 41:109. 1877.
Stanhopea hernandezii (Kunth) Schlechter, Beih. Bot. Centr. 2:490. 1918.

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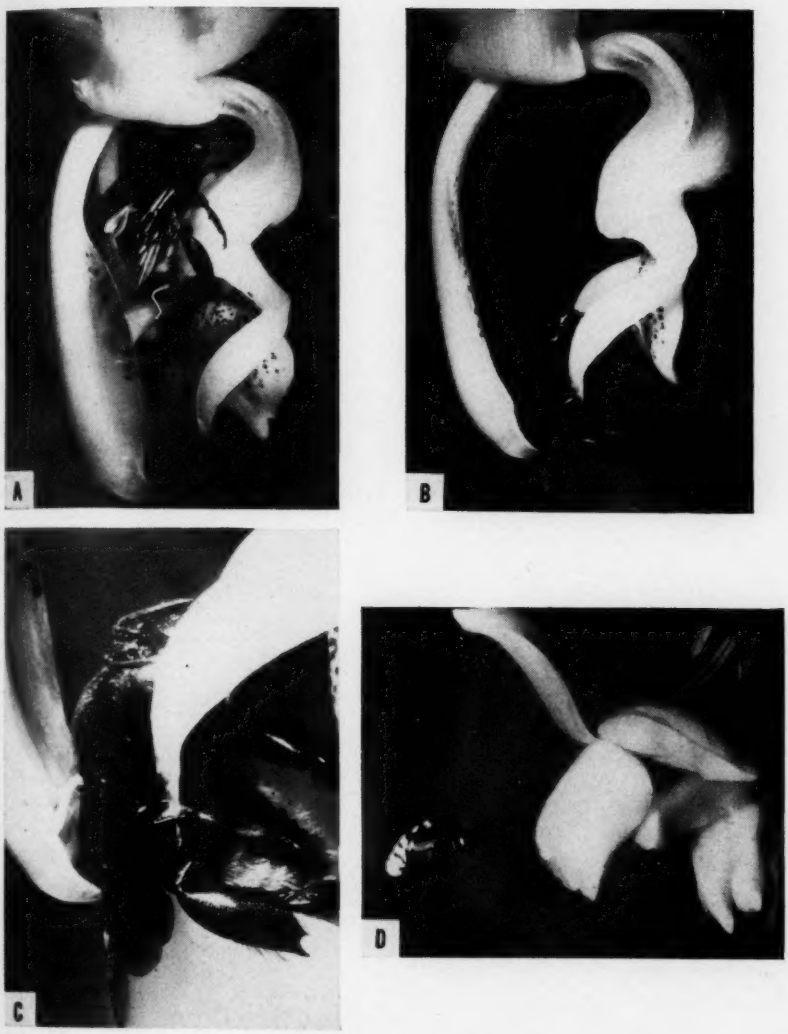
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EXPLANATION OF PLATE

PLATE III

Pollination in *Stanhopea*

A. *Eulaema bomboides* attempting to land on the hypochile of *Stanhopea bucephalus*. B. Bee falling through the flower and engaging the spine of the rostellum under his metathorax. C. Pollinia being inserted into the stigmatic cleft while the bee is falling through the flower. D. *Eulaema moriana* approaching the flower of S. *tricornis*.



DODSON & FRYMIRE—THE GENUS STANHOPEA